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BATHYPELAGIC FISHES AS SOUND SCATTERERS IN THE OCEAN[1]

By

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ABSTRACT

Investigations on the D. S. L. in oceanic waters have been considered in the light of recently acquired data on the structure of the air bladder in bathypelagic fishes. From this it has been suggested that much of the reverberation of supersonic pulses used in echo-sounding may come from layers of these oceanic fishes, particularly from those possessing an air bladder. The following evidence tends to support this: (1) An air bladder is nearly always present in species of the Gonostomatidae, the Sternoptychidae, and the Myctophidae, which are the commonest and most numerous fishes captured in deep-water nets. The dimensions of the air bladder have been listed for a number of species and the possibility of resonant scattering has been discussed. (2) Bathypelagic fishes have an ocean-wide distribution but are poorly represented in Antarctic waters where the D. S. L. has been found to be very sporadic in appearance. (3) A high proportion of species of the three above families have peaks of abundance between 150 and 450 fathoms (274 to 823 metres), the known daytime limits of the D. S. L. (4) Many of these species undertake diurnal vertical migrations.

The existence in the ocean of a deep layer which scatters sound was discovered in 1942 by Eyring, Christensen and Raitt while working for the University of California, Division of War Research. Between 1942 and 1946 a number of anonymous reports, from the Reverbera-

[1] Thanks are due to Dr. G. E. R. Deacon, Mr. F. S. Russell and Dr. H. W. Parker for critically reading this paper.

tion Group and the Sonar Data Division of this research department, contained observations on this reflecting zone, now called the Deep Scattering Layer (D. S. L.) by United States workers. Certain of these findings were discussed by Sewell and Fage (1948) in a paper on the oxygen minimum layer in the ocean.

Recent papers by Raitt (1948) and Johnson (1948) deal with particular aspects of this war-time research, while those of Dietz (1948), Hersey and Moore (1948), and Tchernia (1950) present extensive data on the vertical and horizontal distribution of the D. S. L. These results seem particularly interesting in relation to a survey the writer is carrying out on the comparative biological anatomy of the air bladder in bathypelagic fishes. It is the present intention to give some details of this work and to bring together other evidence which tends to support the suggestion that much of the reverberation of supersonic pulses may be due to reflections from concentrations of bathypelagic species, particularly from those possessing an air bladder.[2]

Any group of organisms suggested as the main scatterers must at least conform to the following main requirements, which are implicit in the work mentioned above.

1. The group must have well defined properties of sound reflection, which includes some degree of concentration in definite strata.

2. Almost certainly, it must have a continuous and nearly ocean-wide distribution.

3. The concentrations of the scatterers must be found between 150 and 450 fathoms (274 to 823 metres) by day.

4. The organisms must show well marked powers of diurnal vertical migration.

These requirements will be discussed in turn, together with other data relevant to each heading.

Johnson (1948), who discovered the diurnal movements of the D. S. L., was the first to try to link it with concentrations of plankton, and he has presented data that show a positive correlation between the depths of the two. He has concluded, however, that this correlation ". . . may be partly secondary, since the more effective scatterers may be larger forms that subsist upon and migrate more or less concurrently with the plankton."

Raitt (1948), from a theoretical analysis based on oscillograph records of single scatterers obtained off Lower California, concluded that most of the total scattering was due to reflection from the larger but less numerous scatterers, with acoustical cross sections between 0.1 and 10 cm^2. In the discussion, after making the tentative sug-

[2] Chapman (1947) has discussed the possibility of tightly packed schools of such fish as louvars being the scatterers.

gestion that ". . . since the scatterers are probably biological organisms with density and compressibility close to that of water, their reflectivity will be low," he goes on to suggest ". . . the possibility of resonant scattering, caused by small gas bubbles in the scatterers or by other properties causing a large difference in compressibility with respect to water. . ."

Dietz (1948) has also drawn attention to scattering by contained air bubbles, but as he and Johnson (1948) noted, they have not yet been found. Similarly, Hersey and Moore (1948), who have considered euphausians as likely scatterers, admit that a serious difficulty ". . . is their small size and the absence of any sort of swim bladder or other associated air bubble to reflect sound."

Although it is often stated that the air bladder is absent or degenerate in bathypelagic fishes, the results of this survey have shown that it is commonly present in the Gonostomatidae, the Sternoptychidae, the Astronesthidae and the Myctophidae. A list of the species so far investigated follows, together with measurements in millimetres of the standard length (S. L.) and the length times the greatest depth of the air bladder (A. B.). Clearly, the two latter measurements will not be those found in the living fish, but it is felt that they are sufficiently approximate to give some indication of the size of this reflecting body in relation to the wave lengths now used in echo-sounding.

GONOSTOMATIDAE	S. L.	A. B.
Gonostoma denudatum Rafinesque	81.0	16.0 x 2.5
Gonostoma elongatum Günther	—	*
Gonostoma bathyphilum (Vaillant)	—	†
Cyclothone signata Garman	21.0	2.5 x 0.8
Cyclothone microdon Günther	—	*
Cyclothone braueri Jespersen & Tåning	—	*
Cyclothone livida Brauer	—	*
Cyclothone acclinidens Garman	—	*
Photichthys argenteus Hutton	141.0	44.0 x 1.0
Vinciguerria attenuata (Cocco)	22.5	3.2 x 1.2
Ichthyococcus ovatus (Cocco)	30.0	4.0 x 1.0
Yarrella blackfordi Goode & Bean	41.0	5.0 x 1.75
Maurolicus muelleri (Gmelin)	43.0	7.0 x 2.5
STERNOPTYCHIDAE		
Argyropelecus sladeni Regan	20.0	1.6 x 1.7
Sternoptyx diaphana Hermann	39.0	9.0 x 3.0
Polyipnus laternatus Garman	32.5	7.0 x 4.0

An air bladder is also present in *Argyropelecus hemigymnus* Cocco (Nusbaum-Hilarowicz [1920]).

ASTRONESTHIDAE	S. L.	A. B.
Astronesthes niger Richardson	56.0	7.5 x 1.0

MYCTOPHIDAE	S. L.	A. B.
Electrona tenisoni (Norman)	47.0	3.5 x 1.25
Electrona antarctica (Günther)	36.0	3.0 x 1.4
Hygophum benoiti (Cocco)	41.0	6.0 x 2.0
Benthosema suborbitale (Gilbert)	24.0	4.3 x 1.3
Benthosema glaciale (Reinhardt)	45.5	5.0 x 1.5
Diogenichthys atlanticus (Tåning)	25.5	3.0 x 0.6
Myctophum humboldti (Risso)	50.0	8.0 x 4.0
Myctophum affine (Lütken)	51.0	10.0 x 4.0‡
Diaphus dofleini Zugmayer	32.0	6.3 x 1.5
Diaphus lütkeni (Brauer)	34.0	3.5 x 0.6
Diaphus garmani Gilbert	34.5	6.0 x 2.0
Diaphus rafinesquei (Cocco)	?	7.0 x 0.8
	(data from Rauther [1922])	
Notolychnus valdiviae (Brauer)	19.0	1.5 x 0.75
Lampadena chavesi Collett	75.0	9.5 x 3.5
Lampanyctus macropterus (Brauer)	65.0	20.0 x 5.5§
Lampanyctus pusillus (Johnson)	22.0	3.5 x 0.5
Lampanyctus alatus Goode & Bean	57.0	9.0 x 2.5
Lampanyctus guentheri Goode & Bean	53.0	9.0 x 2.0
Lampanyctus sp.	32.0	5.0 x 1.0
Ceratoscopelus townsendi (Eigenmann and Eigenmann)	55.0	5.5 x 1.5
Gymnoscopelus nicholsi (Gilbert)	50.0	2.5 x 0.3

An air bladder is also present in *Solivomer arenidens* Miller. It is absent in *Gonichthys cocco* (Cocco) and *Gymnoscopelus braueri* (Lönnberg).

* Air bladder modified into a fat-storing organ in the adult. A normal gas producing bladder probably present in the young stages.

† Air bladder absent.

‡ In a freshly dissected specimen 54.5 mm long, Beebe and Vander Pyl (1944) found the air bladder to be 14.5 x 4.5 mm.

§ Data from Beebe and Vander Pyl (1944) from a freshly dissected specimen.

Thus it will be seen that an air bladder is commonly present in the Gonostomatidae (in 11 of 12 species investigated, but in five it is modified into a fat-storing structure), in the Sternoptychidae (in 4 out of 4), and in the Myctophidae (in 22 out of 24). Furthermore, from the following analysis of catches in the Atlantic (off Bermuda) and in the eastern Pacific, given by Beebe and Vander Pyl (1944), it will be seen that representatives of two of these families constitute over 90% of the specimens taken with net hauls. The Sternoptychidae are listed by Beebe (1937) as third in order of abundance from hauls made off Bermuda.

	Atlantic		*Pacific*	
	Number of specimens	*Relative percentage*	*Number of specimens*	*Relative percentage*
Myctophids	10,008	9.2	10,575	36.9
Cyclothone spp.	95,189	82.2	15,500	54.7
Other fish	10,550	8.6	2,200	8.4
No. of net hauls	1,500		396	

The Bermuda results have been well summarized by Beebe and Crane (1939) who remark ". . . that in number of individuals it is the plankton eaters—*Cyclothone*, myctophids and sternoptychids—that are numerically far ahead of eaters of fish and shrimps, such as the large-toothed stomiatoids (*Stomias*, melanostomiatids, *Chauliodus*, astronesthids, *Idiacanthus*), the lyomerids, large-mouthed pediculates, *Chiasmodon*, etc., . . ." It is, in fact, these fish and shrimp eaters (except for the Astronesthidae) which have lost the air bladder, and as Beebe (1933) found, they generally live in zones which overlap but which are below those of the plankton feeders.

It is certain, however, that net hauls give only a relative conception of abundance, for it is more than likely that at least in the twilight zone of the sea (and probably in the unlighted zone according to Beebe [1934]), fish can actively escape the slow-moving nets. The only direct evidence of the absolute abundance of bathypelagic fish comes from Beebe's (1934) bathysphere work. In comparing his underwater observations with net catches he concluded ". . . that a much more abundant and large-sized fish fauna exists in these waters than is in any way adumbrated by six years of trawling with the best possible oceanographic collecting outfit";[3] this is, as he mentioned earlier, ". . . in the Sargasso sea, which is accounted an arid place for oceanic life."

Concerning stratification in a scattering layer, the works of Jespersen (1935) and Leavitt (1938) have shown quite clearly that populations of bathypelagic fish have a distinct maximum of abundance between the known limits of the D. S. L. Jespersen's analysis of horizontal hauls taken across the Pacific between the Bay of Panama and the Australian region revealed, in addition to a maximum in the upper layers, a well marked maximum corresponding to hauls with 2,000 metres of wire (probably of a depth between 600 and 1,000 metres) and an equally distinct minimum from hauls with 1,000 metres of wire. Similarly, Leavitt's work in the deep water off the

[3] If objection is raised that the switching on of the searchlight from the bathysphere may have attracted the fish (although a number of Beebe's observations do not support this), then they must at least have been in the vicinity to be so influenced.

Woods Hole area showed a peak of abundance of fish populations at 800 metres. It must be added that both workers found that this stratification was much the same for many of the zooplankton organisms.

If bathypelagic fishes are much more abundant than is indicated by net catches,[4] and if they are concentrated during the day in definite strata, which also seems likely from Beebe's (1934) observations, then they may well be the most likely element in the D. S. L. Dietz (1948) recorded that for 18 kc/s sound, the diameter of a resonant air bubble is from 1.5 to 2.5 mm between 150 and 415 fathoms (274 to 759 metres). It may be significant, therefore, that the depth of the air bladder of many of the species earlier recorded lies close to, or within, these limits. The degree of concentration of scatterers along the track of a moving beam (with varying lateral coverage due to the roll of the ship) necessary to produce an echogram trace has yet to be determined, but apparently it need not be of a high order, judging from Raitt's (1948) analysis.[5]

The works of Dietz (1948), Hersey and Moore (1948) and Tchernia (1950) show clearly that any group of organisms considered to give rise to a D. S. L. must have (1) a distribution that gives the appearance of a continuous trace on the recording paper, and (2) an almost ocean-wide occurrence. Concerning the latter, the results of oceanographic expeditions, taken as a whole, do not suggest that bathypelagic fish populations have any major discontinuities in distribution (except in Arctic and Antarctic waters). For example, we may consider the station list given by Brauer (1906). The number of stations in the Atlantic and Indian oceans where midwater nets were fished was 78, of which 72 gave positive results. Of the latter, 65 contained combinations of species known to have an air bladder.

[4] Additional evidence of the abundance of some of these fishes may be gained from an analysis of the stomach contents of their predators. Legendre (1934), who made an intensive study of the food of *Germo alalunga* in the Bay of Biscay area, found that, next to the amphipod *Brachyscelus crusculum*, the gonostomatid fish *Maurolicus muelleri* (Gmelin) was the most frequent and numerous in the stomach contents. He argued that the presence of hundreds of *Maurolicus* in *Germo* stomachs suggests that it is not only abundant but must live in dense concentrations. Chapman (1943) noted that the main feeding grounds of the fur seal while on the Pribilof and Komandorskie rookeries are outside the 100 fathom line and that it feeds extensively on fishes of the genus *Bathylagus*, which is poorly represented in collections. Davies (1949) has shown that myctophids (particularly *Myctophum humboldti*) are a very important part of the food of *Merluccius capensis*, *Zeus capensis* and *Brama raii* in deep water off the western shores of South Africa.

[5] Tester (1943) found that a record of herring could be obtained by echo sounder even when the fish were thinly scattered. But this was in shallow water.

Continuity in recording the D. S. L. would appear to be the stumbling block to any biological hypothesis. Even small scale patchiness would be detected on an echogram. It is because plankton populations are limited in space and time that Tchernia has criticized the plankton hypothesis.

Concerning continuity in bathypelagic fish populations, little is known. To investigate this thoroughly would mean an enormous amount of work with much more efficient catching gear than is available at present. Perhaps certain tentative conclusions may be drawn from Jespersen's (1935) analysis of DANA stations in the Pacific. Considering only the deep-lying maximum in numbers of fish (from hauls with 2,000 metres of wire), the mean catches per one hour's tow from stations in the eastern Pacific were five or six times greater than those obtained from the western half. Striking also is the good agreement between the different groups of stations when these two areas were considered apart. Considering the eastern Pacific, the average catch from the Bay of Panama was 523, and that from the section between Panama Bay and the Marquesas Islands was 633. From eight different sections in the western Pacific the average numbers range from 85 to 156. If bathypelagic fish populations are patchy in distribution, then these figures might be expected to differ by larger factors, particularly since the averages for each section are calculated from few hauls (eleven was the most, one the least), each haul representing only the sampling of a few miles of sea.

It may be added also that species of *Cyclothone* were prominent in the catches, and of these fish Beebe (1933) has stated: "Whereas Cyclothones compose four-fifths of all the fish trawled above 400 fathoms, yet I am convinced that they do not live in schools; there is too great a uniformity of numbers in each net drawn." Furthermore, he did not observe large schools of hatchet fish or myctophids during his bathysphere dives. Thus there is some evidence (but admittedly insufficient) to show that certain bathypelagic fish do not occur in dense aggregations. If they are the scatterers and are concentrated in a layer about 100 metres thick during the day, a record which appears continuous on an echogram may not be impossible.

However, the D. S. L. is not found everywhere in deep oceanic water. Dietz (1948) records that it disappeared after crossing the Antarctic Convergence ". . . and was rarely ever well developed in Antarctic waters." Tchernia (1950) also found the D. S. L. to be absent in Antarctic waters, but his records suggest that it disappeared at the northern limit of pack ice and not at the Antarctic Convergence. If euphausians or squid are the main scatterers, as suggested by Hersey and Moore (1948) and Lyman (1948) respectively, this dis-

continuity is rather surprising, for these organisms are known to be very abundant in the Antarctic area.

At first it seemed possible that this sudden disappearance of the D. S. L. could be simulated by a sharp change in the vertical distribution of the scatterers, that is, by those south of the Convergence living at sufficiently higher levels to be undetected due to masking of echoes by the outgoing signal trace. But if macroplankton organisms are the scatterers, this does not seem likely from the results of Mackintosh's (1937) report. During the summer months he found the greatest concentrations of macroplankton between the surface and 250 metres, north as well as south of the Antarctic Convergence.

Dietz (1948) has tended to link the nonformation of the D. S. L. in the Antarctic with the almost permanent daylight during summer. It is difficult to see how the one can be related to the other, for if daytime conditions are extended one might expect a parallel extension of the time the scattering layer is recorded. Even if the bulk of the macroplankton live between the surface and 250 metres, some indication of part of these relatively abundant populations might be expected, if they have scattering properties.

If fish are considered to be the scatterers, these findings seem less puzzling. There are few species of bathypelagic fishes in Antarctic waters, about 20 being recorded, mostly from the extensive surveys of the Discovery Committee's research ships. Of these, *Bathylagus antarcticus*, *Paralepis coatsi*, *Gymnoscopelus braueri*, *Cyclothone microdon*, *Electrona antarctica* and *E. tenisoni* are the most common, and only the three latter possess an air bladder.

Actually there is no marked decrease in the number of species on entering Antarctic water, for this decrease is spread over latitudes 40° to 60°, being most pronounced between latitudes 50° to 60°. Those species which do extend into the Antarctic are by no means abundant. For example, about 150 specimens of *Electrona antarctica* (the commonest species in net hauls, except perhaps for *Cyclothone microdon*) have been taken from over 2,000 Discovery stations south of 50° S. This may be compared with the catches of *Myctophum affine* from the eastern tropical Pacific, listed by Beebe and Vander Pyl (1944); here only 31 stations yielded 3,706 fish. Thus there would appear to be some degree of correlation between the distribution of the D. S. L. and that of bathypelagic fishes. If they are the main scatterers, a sporadic development of the D. S. L. in Antarctic waters might be expected.[6]

[6] On this reasoning, one would similarly expect the D. S. L. to be sporadically recorded in Arctic and Subarctic water, which are similarly lacking in numbers of species and individuals of bathypelagic fishes.

The third requirement may be discussed more briefly, since, in considering the stratification of deepsea fish populations, mention has already been made of the findings of Jespersen (1935) and Leavitt (1938), which show peaks of abundance between the known daytime limits of the D. S. L. Murray and Hjort (1912) found that the abundant fishes, such as *Cyclothone signata* and certain species of Sternoptychidae and Myctophidae, have centres of concentration between 200 and 500 metres.

This is further substantiated by an analysis of the catches from the Discovery Committee's vessels; a part of these catches was studied by Norman (1930). Nine out of ten myctophids, and all six of the gonostomatids investigated, all being common in the catches, have centres of abundance between 200 and 1,000 metres. Many of the myctophids taken by the ARCTURUS and reported by Beebe and Vander Pyl (1944) show populations living between the surface and the daytime levels of the D. S. L.

Finally there is the well marked vertical migration of this reflecting layer. Brauer (1906, 1908) mentions a number of fishes which live by day in the twilight zone between 200 and 400 metres but which appear in the upper layers at night. Murray and Hjort (1912) gave evidence suggesting a vertical migration in such fish as *Gonostoma elongatum*, *Photostomias guerni*, *Astronesthes* and *Idiacanthus*. For the sternoptychid fishes *Argyropelecus hemigymnus* and *A. olfersi*, taken in the Mediterranean and the Atlantic, Jespersen (1915) found a maximum of abundance between 300 and 600 metres by day, but at night both species were taken comparatively near the surface. Tåning (1918), while noting an obscuring factor in the avoidance of nets by scopelid fishes during the day, tentatively concluded that they are twilight fishes, with limited day and night migrations; he suggests, for example, a migration of 500 metres for *Benthosema glaciale*. Beebe and Vander Pyl (1944) concluded that numerous myctophids are nocturnal surface swimmers, descending to deeper layers during the hours of daylight.

More precise information on the vertical migrations of bathypelagic fishes is certainly needed. The time of ascent and descent of the D. S. L. seems to be only an hour or less before sunset and sunrise, from which data it might be possible to get some indication of the nature of the scatterers. For example, these times of movement do not fit very well with what is known of the migrations of oceanic zooplankton organisms. For instance, the investigations of Waterman, et al. (1939) on diurnal movements of deep-water plankton show that "Before sunrise most of the animals had already descended about half their total downward distance, and several such as *Boreomysis*,

Eucopia and *Parapasiphäe,* had reached the deepest point in their migration by sunrise."

For bathypelagic fishes, the closely spaced hauls made during the Arcturus expedition in the eastern Pacific seem to be the only ones ever taken with some purpose of studying vertical migrations in this group. Discussing the data for the very abundant *Myctophum coccoi,* Beebe and Vander Pyl (1944) stated: "This slender-tailed lantern fish comes up from rather shallow depths just after dark on the equator and rapidly reaches its greatest abundance, or perhaps at this time 8–9.30 p. m., keeps in very dense, compact schools. Throughout the night its numbers in the nets decrease, probably from a general scattering in search of food and the last individual dives into darker levels at 6.30 a. m. at the very latest." They also remarked on the suddenness with which this downward migration began. The correspondence with the movements of the D. S. L. appears quite good, but clearly more data are desirable before any firm conclusions can be drawn.

The speed of the upward and downward migrations of the D. S. L. has been considered previously as a possible pointer to groups of organisms which may give rise to it. Johnson (1948), obtaining a maximum rate of 8 feet per minute, concludes that some of the larger more active zooplankton organisms can swim quite comfortably at this speed. Dietz (1948) obtained rather higher rates of movement but decided that they were ". . . more suggestive of the general zooplankton than of faster swimming fish." Yet the more common fish have to contend with an air bladder, and in migrating upwards they must limit the rate of climb in order to avoid excessive expansion of the gases in the air bladder. Conversely, in moving downwards, the rate of descent must be slow enough to enable equilibrium to be reached with the increasing hydrostatic pressure.

Parr (1937) has considered the functioning of the air bladder in the deepsea environment, and from calculations made from the energy of compression equation, $E = RT \log e\, P2/P1$ (where $P2/P1$ is the ratio of partial pressures), he found that the energy required to attain an equivalent degree of buoyancy at 1,000 metres is 300 times the amount needed at 10 metres.

Assuming 50 metres per 15 minutes as the rate of descent, and assuming the scatterers to be fish, we have the following relationships. In moving downwards from 10 to 60 metres during the first 15 minutes the increase in energy necessary to attain equivalent buoyancy at 60 metres is about 10 times that required at 10 metres. After half an hour the fish will be at 110 metres, and here the factor-of-energy increase relative to that at 60 metres must be 2.2. After three-

quarters of an hour the fish will be at 160 metres, and now only 1.6 times as much energy is required compared to the amount necessary at 110 metres; and so the factor gradually decreases. The physical limitations may thus be less serious than Parr supposed.[7]

However, it is clear that the greatest energy increase is needed during the first part of the descent; conversely, during the latter part of the ascent the relative decrease in hydrostatic pressure will be greatest. Thus it may be possible that there is a slowing up of the rate of migration in the upper reaches of the sea. A graph drawn by Hersey and Moore (1948), plotting time against the depth of the D. S. L. around sunset, does show some flattening at the upper levels, but clearly it will be best to leave the discussion of this possibility until more observations are available.

Finally it may be mentioned that the depths at which bathypelagic fishes are found are probably dependent on local, seasonal and latitudinal variations in illumination parallel to those found by Dietz (1948) and Hersey and Moore (1948) for the variations in depth of the D. S. L. No emphasis has been placed on this, however, as it also applies to at least certain macroplanktonic organisms with well developed eyes.

DISCUSSION

The measurements of air bladders of a number of bathypelagic fishes (see p. 3–4) may now be amplified further. In any species the diameter of the air bladder will increase in size from a fraction of a millimetre in the post-larvae to its full growth in the adult. At what particular stage in the life history it begins to function is not known, but De Jong (1936) found in post-larval cod (6.5 mm) that the nuclei of the gas gland had a peculiar appearance. From this he assumed that it had begun to function. In young stages of *Cyclothone microdon* (8 mm) the air bladder is about 0.5 mm in length, is oval in outline, and has what appears to be a relatively large gas gland fed by well defined retia mirabilia. In the adult these are quite degenerate and, as already indicated, the tissues of the bladder are charged with fat. Probably in all adult *Cyclothone* spp. with a fat-charged air bladder there is a period during the post-larval life when the air bladder contains gases; this may well mean that the younger stages are more

[7] To this may be added the fact that presumably more energy can be diverted to the gas-secreting structures during the descent, since less is required in muscular effort. Furthermore, compared to fishes living above the continental shelf, the retia mirabilia and gas glands are extremely well developed in bathypelagic fishes; also, in general their air bladders are relatively smaller compared to the size of the body cavity.

effective sound scatterers than the adults. It should also be added that adult *Cyclothone* do not appear to undertake diurnal vertical migrations. Perhaps this may not apply to advanced post-larvae which have means for regulating their specific gravity.

However this may be, it is known that during growth the post-larval stages begin to move downwards, and at the metamorphosis from post-larva to adolescent there appears to be a rapid migration much nearer to adult levels (see Jespersen and Tåning [1926]). Perhaps differences from adult behavior during the adolescent phase may be the explanation of multiple scattering layers.

Thus we may conclude that within the limits of the scattering layers there is, as it were, a population of air bladders in any one species with the smaller sizes more numerous than the larger, owing to the differential mortality during the life history. Equally, there will be variations from species to species. Such an assemblage of sound scatterers might be expected to give a good return of echoes for a range of frequencies.

Merriman (1949) has suggested, however, that the bulk of the scatterers are likely to be zooplankton organisms, since minute particles are known to scatter high-frequency sound. If he is referring to the experiments of Dietz (1948) with clouds of sand grains, the writer would like to suggest that such a conclusion is not yet justified. The experiments only prove that sand grains, with very different values of compressibility and density from living organisms, can act as scatterers. Furthermore, it is possible that the particles may drag down with them a certain amount of air which would greatly enhance their powers of returning echoes. However, should bathypelagic fishes prove to be the main scatterers, Merriman's conclusions concerning echo-sounding and the discovery of major fishery resources in deep waters need hardly be modified.

It is unfortunate but understandable that such a technique for exploring the oceans should find the marine biologist with so incomplete a knowledge of the quantity of life in the deep sea and hence without some estimate of the numbers of organisms covered by a sound beam. However, the recent work of Riley, Stommel and Bumpus (1949) has done much in advancing our understanding of this aspect of oceanography. It seems clear that the over-all production of phytoplankton in deep oceanic water may be much the same as that of coastal or bank areas, but owing to its greater vertical disposition, more energy is expended by the herbivores in feeding on it. The effects of this will be reflected in each level of the food chain, and, as these workers say, it would lead to a "progressive attenuation" of the higher members.

Most of the deepsea fishes with air bladders are but one stage removed from the herbivores, since they feed particularly on copepods.

The degree of attenuation at the higher levels of the food chain can be seen from the figures given by Beebe (1937) for his Bermuda hauls, although allowance must be made for the greater ease with which some of the fish-eaters escape from nets. Starting with the families which feed particularly on copepods, the Gonostomatidae, Myctophidae and Sternoptychidae (some of which are known to eat fish), and then following with families which prey on fish (and prawns), we have the following numbers caught: smaller Gonostomatidae (including the Maurolicidae): 95,624; Myctophidae: 10,008; Sternoptychidae: 2,464; Chauliodontidae: 793; ceratioid angler fish: 337; Melanostomiatidae: 239; Malacosteidae: 141; Alepocephalidae: 128; Stomiatidae: 119; Eurypharyngidae: 84; Astronesthidae: 62; and Chiasmodontidae: 36. This gives a rough figure of 50 smaller plankton-eating fish to one large fish-eater, although the ratio is no doubt smaller than this due to the differential escape factor mentioned above and to the fact that only the more important fish-eating families have been listed. This ratio looks remarkably small, but it should be noted also that very few of these higher members of the food chain reach a length greater than 250 mm, although it is likely that in general they range to rather larger sizes than net catches indicate.

That there is a considerable degree of attenuation at the higher trophic levels may be reasonably inferred. As previously mentioned, nearly all fishes at these levels have lost the air bladder and few appear to undertake vertical migrations.

Returning to the smaller vertically-migrating plankton-feeding fishes with air bladders which, if bathypelagic fish are the scatterers, must be the main source of echoes, these take advantage of the greater concentrations of zooplankton in the surface layers, but in order to do so they must expend considerable energy in reaching the upper 100 metres and then must expend more in order to obtain sufficient food, since the concentrations must preclude efficient filter feeding. However, Riley, Stommel and Bumpus (1949) have figures showing that the mean volume of crustacean plankton in the upper 100 metres of the Sargasso Sea is about one-third that in the coastal area from the surface to the bottom. It seems not unreasonable to conclude that these waters may support a fairly numerous population of small fishes.

In conclusion, it hardly needs to be emphasized that the foregoing is no more than an attempt to substantiate an hypothesis, but it is hoped that enough evidence has been brought forward to justify consideration of bathypelagic fishes as scattering organisms. Perhaps varying combinations of these fishes with other oceanic organisms may

prove to be responsible for the D. S. L. Owing to the limited catching power of deepsea gear it will not be easy to test this; none the less, combined biological and physical observations over a period of time may be expected to give some indication through a process of elimination. At all events it is to be hoped that the nature of the scattering layers will soon be found so that full use can be made of this valuable technique for exploring the ocean.

SUMMARY

Investigations on the D. S. L. in the ocean have been considered in relation to recently acquired data on the structure of the air bladder in bathypelagic fishes. From this it has been suggested that much of the reverberation of supersonic pulses used in echo-sounding may come from concentrations of these oceanic fishes. The following evidence tends to support this:

1. It has been found that an air bladder is nearly always present in species of the Gonostomatidae, the Sternoptychidae, and the Myctophidae, which are the commonest and most numerous fishes taken in net hauls. Furthermore, it is highly likely that they are much more numerous than is indicated by collecting gear.

The presence of an air-filled structure should make these organisms strong scatterers of supersonic sound. In relation to the wave lengths now used in echo-sounding, the dimensions of the air bladders are listed.

2. Bathypelagic fishes have an ocean-wide distribution but are poorly represented in Antarctic waters. The latter may explain why the D. S. L. is rarely found south of the Antarctic Convergence. Little is known concerning the continuity of deep-living fish populations, but there is some evidence to indicate that they are fairly uniformly distributed over wide areas.

3. A high proportion of species of the three families mentioned earlier are known to have peaks of abundance between 150 and 450 fathoms (274–823 metres), the known day-time limits of the D. S. L.

4. Many of these species undergo diurnal vertical migrations. The little evidence available suggests that the timing of these movements coincides with those of the scattering layer. The rate of migration is considered in relation to the functioning of the air bladder, this indicating that the physical limitations of hydrostatic pressure change are less serious than might be supposed but that the rate of migration, whether upward or downward, may be slower in the upper layers of the sea.

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THE EXCHANGES OF FRESH AND SALT WATERS IN TIDAL ESTUARIES[1]

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ABSTRACT

An empirical theory is presented which describes the exchanges between various parts of an estuary as a result of tidal oscillations, and which permits the calculation of the average distribution of fresh and salt water within the estuary. The characteristics of the estuary used in the calculations are the mean range of tides, the river flow, and the topography, all readily available for most estuaries.

The calculations are shown to produce results which are similar to distributions observed in three very different estuaries. The theory will permit calculation of the changes in distribution of salinity and fresh water in any given estuary to be expected as a result of variation of river flow.

INTRODUCTION

In studies of the ecology of tidal estuaries the exchanges of fresh and salt water are of primary importance in determining the character of the environment. Thus, for example, the distribution of salinity and the extreme conditions to which sedentary organisms will be exposed are determined by these exchanges. The distribution of planktonic populations, of eggs spawned within the estuary, of pollutants introduced by cities or industries, in short, the distribution of any material dissolved or suspended in the water, is determined by the circulation of fresh and salt water and by the exchanges between various parts of the estuary. These exchanges, and the resulting distributions, are related in a regular way over short periods of time to the tidal oscillations and over longer periods of time to fluctuations of river flow. They are likewise related in more erratic ways to the effects of winds.

Although numerous estuarine studies have been made, the theoretical basis of the circulation is only slightly understood. Interpretation of survey data is improved by using the river water as a tracer to determine exchange ratios, flushing times and nontidal drifts (Tully, 1949; Ketchum, 1950; Ketchum, Redfield and Ayers, 1951).

In this paper an empirical theory is presented which describes the exchanges across various cross sections and which permits the calcu-

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lation of the resulting average distribution of fresh and salt water in an estuary. The exchanges of any other property of the water can be derived in a similar way. The data used in the calculations are tidal heights, river flow and the topography of the basin, all readily available on most important estuaries. The calculation is applied to three estuaries, and the hydrographic conditions which influence the results of the calculation are discussed.

SIMPLIFYING CONCEPTS

An estuary is defined as a region where river water mixes with, and measurably dilutes, sea water. The theory attempts to predict average conditions in successive volume segments of an estuary for a constant rate of river flow and the mean tidal range. Variations in the horizontal distribution of fresh water within a cross section, such as are commonly found as a result of Coriolis' forces, are neglected. The effects of vertical stratification will be discussed below.

The following simplifying concepts are involved:

1. *Steady State Distribution.* It is assumed that there is a steady state distribution of fresh and salt water within the estuary. This is obviously true for long periods of time, since estuaries are not becoming either fresher or more saline. At times of changing runoff of the rivers, however, the average distribution within the estuary changes, and the steady state distribution cannot be assumed.

In order to maintain a steady state the following conditions must be met at every complete cross section of the estuary:

a.) *Salt:* There must be no net exchange of salt during a tidal cycle across the section. This, of course, does not mean that the circulation of salt water is zero but that there is a balance between the inflow and outflow of sea water.

b.) *Fresh water:* During a tidal cycle there must move seaward a volume of fresh water equal to the volume introduced by the river in the same period of time.

2. *Inner End of Estuary.* The inner end of the estuary is defined as the section above which the volume required to raise the level of the water from low to high water mark is equal to the volume contributed by the river during a tidal cycle. There will be no net exchange of water through this section during a flood tide, since the entire rise of tide above the section is contributed by river flow. During the ebb tide there will be a loss through this section of one river flow per tide. Since there is no exchange on the flood tide the water above this section should be completely fresh. It will be noted that this is a

dynamic, not a geographic definition, since the boundary will move corresponding to changes in river flow.

3. *Segmentation of the Estuary.* The above paragraph defines a section which is the seaward boundary of the innermost volume segment of the tidal portion of the river. This is called Segment 0. Consecutive volume segments are defined so that the distance between their inner and outer boundaries is equal to the average excursion of a particle of water on the flooding tide. The average excursion is derived from the volume entering each part of the estuary on the flooding tide as well as the topography of the estuary. If the volume entering on the flooding tide were to act like a piston, displacing and pushing upstream its own volume of water from the next landward segment, the distance moved would be the average excursion of a particle of water on the flood tide in that part of the estuary. The segment so defined would contain, at high tide, a volume equal to that contained in the adjacent seaward segment at low tide. Consequently, along the length of the estuary each segment is so defined that the high tide volume in the landward one is equal to the low tide volume in the adjacent seaward one. Beginning with Segment 0, defined above, the entire estuary can thus be subdivided into a series of volume segments.

With R as the volume of river water introduced during a tidal cycle, P the local intertidal volume[2] and V the low tide volume of each segment, the following equations summarize these fundamental definitions:

1. The inner end of the estuary is defined as the section above which $P_0 = R$.

2. The limits of each successive volume segment are placed so that

$$V_1 = V_0 + P_0,$$
$$V_2 = V_1 + P_1 = V_0 + P_0 + P_1,$$
$$V_3 = V_2 + P_2 = V_0 + P_0 + P_1 + P_2 \text{ etc.}$$

It will be noted that the low tide volume in each segment equals the total tidal prism within the inner boundary of the segment, plus the low tide volume in Segment 0; that is,

$$V_n = V_0 + \Sigma_0^{n-1} P,$$

or, since $P_0 = R$: $\qquad V_n = V_0 + R + \Sigma_1^{n-1} P.$

[2] The tidal prism is defined as the volume of water required to produce the observed rise in water level in the estuary on the flooding tide. The part of the total tidal prism in each segment at high tide is called the local intertidal volume.

THE EXCHANGE RATIO

The estuary is divided into volume segments defined as above, so that the limits of each segment show the average excursion of a particle of water on the flood tide. If it is assumed that the water within such a volume segment is completely mixed at high tide, the proportion of water removed on the ebb tide will be given by the ratio between the local intertidal volume and the high tide volume of the segment. This same proportion of river water and of anything dissolved or suspended in the water will be removed by the ebb tide. Thus, an exchange ratio (r) can be defined for each segment (n):

$$r_n = \frac{P_n}{P_n + V_n}.$$

The effect of incomplete mixing on the exchanges will be discussed below.

The river water present in each segment is a mixture of river water accumulated during many tidal cycles. Each segment receives on each tidal cycle a volume of river water (R) equal to the volume introduced by the river in the same period of time. If we take R_1 as the volume of river water arriving during the current tidal cycle, then the amount removed on the ebb tide will be rR_1, and the amount remaining behind will be $(1 - r)R_1$. This same proportion of river water (R_2) arriving on the previous tidal cycle was left behind by the previous ebb tide, and the amount of this river water (of age two tidal cycles) removed will be $r\,(1 - r)R_2$ and the amount of this water remaining, after being depleted by two successive ebb tides, will be $(1 - r)^2\,R_2$. The proportion of water of various tidal ages removed, and remaining behind, as a result of the exchanges on any given ebb tide may be summarized as follows:

Age in Tidal Cycles	*River Water Removed*	*River Water Remaining*
1	rR_1	$(1 - r)\,R_1$
2	$r\,(1 - r)\,R_2$	$(1 - r)^2\,R_2$
3	$r\,(1 - r)^2\,R_3$	$(1 - r)^3\,R_3$
m	$r\,(1 - r)^{m-1}\,R_m$	$(1 - r)^m\,R_m$;

here 1, 2, 3 . . . m represent the number of tides each portion of the river water has been within the segment considered.

If the river flow is constant, all values of R are equal and the steady state condition can be assumed to exist. The total volume (Q_n) of river water accumulated within any volume segment (n) of the estuary at high tide is then the sum of the remaining volumes given in the

final column above. Since the equation is written for the high tide condition, one volume of the river flow which has not yet been depleted is also present; that is,

$$Q_n = R\{1 + (1 - r_n) + (1 - r_n)^2 + (1 - r_n)^3 + \ldots + (1 - r_n)^m\} .$$

As m becomes large, this series will approach the limit

$$Q_n = R\,\frac{1 - (1 - r_n)^m}{r_n} .$$

Since $(1 - r)$ is always less than unity, $(1 - r)^m$ approaches zero after an infinite number of tidal cycles, and the sum can be reduced to

$$Q_n = \frac{R}{r_n} .$$

It will be remembered that one qualification of the steady state distribution was that the river water passing seaward through each cross section on each tidal cycle must equal the volume of river water (R) introduced during the same period of time. The above relationship states that the volume of river water moving seaward is the product of the exchange ratio and the accumulated volume of river water (rQ). It is readily seen that this product equals R, so that this criterion of steady state distribution is satisfied.

The exchange ratio is defined on the assumption of complete mixing of the volume of water in each segment at high tide. The average excursion of water during the flooding tide is presumed to set the upper limit of the length of the estuary over which complete mixing can be logically assumed. It is for this reason that the subdivision of the estuary is essential in the application of the theory.

Incomplete vertical mixing can be detected readily if salinity observations are available, since the water diluted by river effluent will be limited to the upper layers of the water column. Only the mixed volume of water should be considered in such a case, and the exchange ratio applicable would be

$$r'_n = \frac{P_n}{P_n + V_n} \times \frac{D}{H} ,$$

in which D is the average depth of the Segment n and H is the depth of the mixed layer. The exchange ratio so calculated will be greater, and the resulting accumulation of river water (Q) will be smaller than would be obtained if the entire depth were used. In such a case the segmentation of the estuary is also made using volumes computed to the mixed depth. The entire treatment is developed, therefore, as

though the water below the mixed zone had no part in the tidal mixing process and could be replaced, without changing the distribution, by a false bottom.

Incomplete horizontal mixing will also modify the distributions to be expected. The effects are not incorporated into the theory since there are no independent criteria to evaluate their magnitude. The effects of incomplete horizontal mixing will be discussed qualitatively below.

EXCHANGES IN A MODEL ESTUARY

The exchanges in a theoretical estuary, rectangular in cross section, in which the depth at low tide is half of the high tide depth (i. e. $P = V$), will be calculated in order to indicate how the theory is applied. The results are presented in Table I. For every volume segment the exchange ratio is 0.5, and the accumulation of river water is $2R$. Taking R as unity, the volume enclosed in Segment 0 at high tide is 2, which is all river water—100% fresh. In Segment I, having a relative high tide volume of 4, half of the water is river water. On the ebb tide Segment I receives one volume (all of it fresh water) from the river (Segment 0) and loses 3 volumes ($P_0 + P_1$) at a concentration of 50% fresh water (1.5 volumes of river water) to Segment II. At low tide, therefore, Segment I contains 2 volumes, three-quarters of which is river water. On the flooding tide Segment I loses no water landward, since, above its inner limit, river flow is sufficient to provide the observed rise in water level. It receives from the adjacent seaward segment two volumes which contain 25% river water. The high tide content is thus returned to the original condition. The net result of the tidal oscillation has been to add to Segment I a volume of river water from the river, and to move an equal volume of river water from Segment I to Segment II. Similar treatments, shown for the river boundary and for the first four segments, can be expanded to the nth segment with the same net seaward transport of river water through every cross section. The fact that each segment returns to its original high tide content shows that the net exchange of salt during a tidal cycle is zero, and thus the steady state requirements are satisfied.

A basic assumption of the theory is that the mixing is complete within volume segments defined by the average excursion of a particle of water on the flooding tide. For each segment in Table I, complete mixing of the volumes of water added during the tidal cycle will produce mixed water of the same characteristics as the water present at high tide. In Segment I, for example, one volume of water is added on the ebb tide and two volumes on the flood tide. These three

volumes contain a total of 1.5 volumes of river water. If they were mixed together the composition would be 50% fresh water—the same composition as the high tide content of the segment. However the mixing may be accomplished, the net effect of the mixing processes must be equivalent to the mixing of the volumes of water added to each segment during a tidal cycle if the theory is reliable.

APPLICATION TO NATURAL ESTUARIES

The total accumulation of river water has been calculated by the above method for Raritan River and Bay, New Jersey, for Alberni Inlet, B. C., and for Great Pond, near Falmouth, Massachusetts. These three estuaries are different in almost all characteristics. In all three, survey data are available which permit calculation of the fresh water content from the salinity distribution, so that the results of the survey and of the calculation can be compared. The method used, and described here for Raritan Bay, is similar for the other two locations.

Raritan River and Bay, New Jersey. A survey of Raritan River and Bay was made in December 1948, which permits comparison of the computed distribution of fresh and salt water with the observed distribution over a length of about 20 miles of the estuary. Raritan River and Bay have sandy or marshy shores, a maximum depth of 40 feet in dredged channels, and they vary in width from 0.1 to 7.0 miles. The surface area of the surveyed portion of the estuary was 1,670 million square feet, or about 45 square nautical miles. Since the mean range of tides is 5.5 feet, the total volume of the tidal prism is 9,200 million cubic feet. This is almost 300 times greater than the volume introduced by the river during a tidal cycle at the time of our survey.

In the Bay the average salinity for each of five cross sections was determined from the results obtained at 4 to 7 stations. These stations were occupied once each hour throughout the complete tidal cycle. The high tide data are used for comparison with the theory. In the river the results of a single station, occupied at high tide, was used to determine the average salinity across each section. The method used for calculating the distribution of fresh water from the salinity observations has been described by Ketchum, 1950.

The first step in the application of the theory is to determine the total low tide volume of the estuary enclosed by various cross sections. This is done by drawing numerous cross sections with the aid of a navigation chart and determining their cross-sectional area with a planimeter. The volume is computed by multiplying the distance

TABLE I. Net Exchanges in a Model Estuary as a Result of Tidal Oscillations and River Flow
(all volumes expressed as multiples of river flow).

Segment	*0*		*1*		*2*		*3*		*4*	
Intertidal volume (P_n)	1		2		4		8		16	
High tide volume ($P_n + V_n$)	2		4		8		16		32	
Exchange ratio (r_n)	0.5		0.5		0.5		0.5		0.5	
River water content (Q_n)	2.0		2.0		2.0		2.0		2.0	
% Fresh	100		50		25		12.5		6.25	
EBB TIDE EXCHANGES	Vol.	Fresh	Vol.	Fresh	Vol.	Fresh	Vol.	Fresh	Vol.	Fresh
Landward	0	0	+1.0	+1.0	+3.0	+1.5	+ 7.0	+1.75	+15.0	+1.875
Seaward	−1.0	−1.0	−3.0	−1.5	−7.0	−1.75	−15.0	−1.875	−31.0	−1.9375
Net change	−1.0	−1.0	−2.0	−0.5	−4.0	−0.25	− 8.0	−0.125	−16.0	−0.0625
FLOOD TIDE EXCHANGES										
Landward	+1.0	+1.0	−0	−0	−2.0	−0.5	− 6.0	−0.75	−14.0	−0.875
Seaward	0	0	+2.0	+0.5	+6.0	+0.75	+14.0	+0.875	+30.0	+0.9375
Net change	+1.0	+1.0	+2.0	+0.5	+4.0	+0.25	+ 8.0	+0.125	+16.0	+0.0625

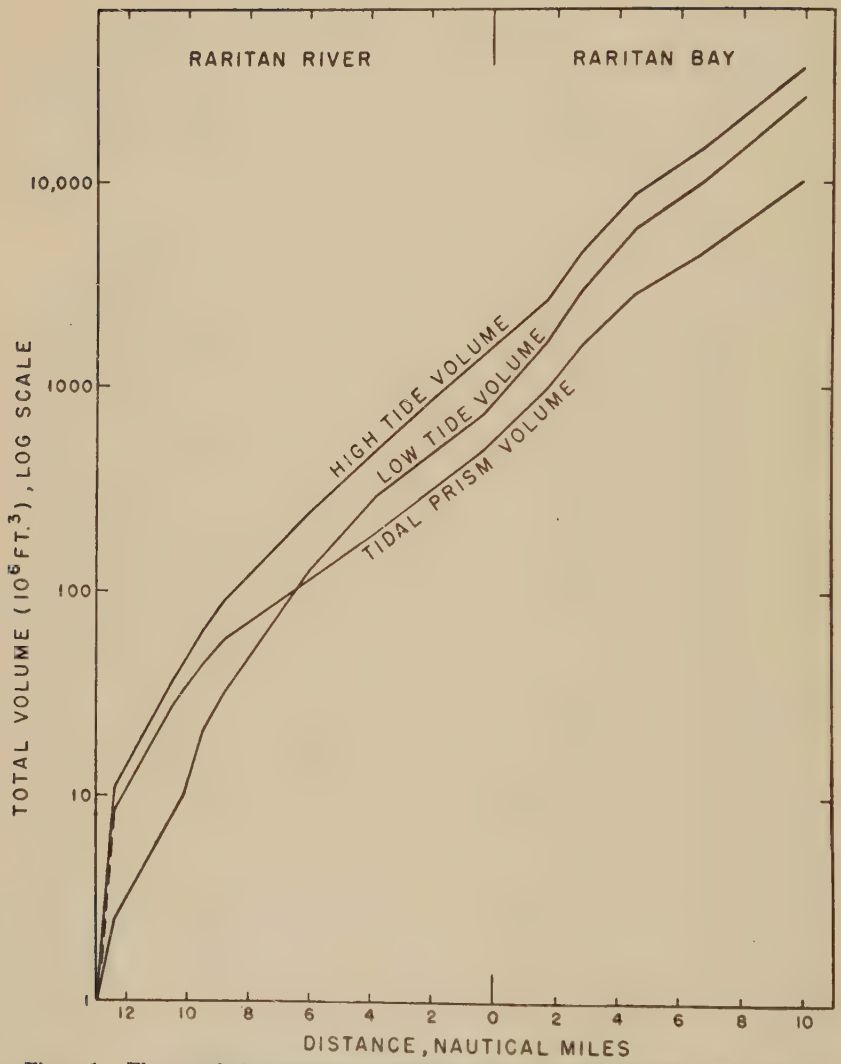

Figure 1. The cumulative volumes of water at low tide, high tide, and in the tidal prism enclosed by various cross sections in Raritan River and Bay. The river end of the estuary is at the left. (The semi-log scale is used for convenience only.)

between sections by the average of their cross-sectional areas. The cross sections drawn should be selected so that the change in width and depth of the estuary between sections is as uniform and gradual as possible. The sum of the volumes enclosed at low tide by each

section is determined and plotted against the length of the estuary, as in Fig. 1.

The volume of the tidal prism is computed from the chart and from the tide tables using the mean range of tides. This volume is also plotted against the length of the estuary. The sum of these low tide and tidal prism volumes gives the high tide volume enclosed by each section, which is calculated and also plotted.

Determination of the segmentation of the estuary is illustrated in Table II for the average river flow that obtained during the survey conducted in December 1948 (33×10^6 ft.^{3}/tidal cycle). The distance at which the volume of tidal prism is equivalent to the river flow per tide (P_0) is read from the graph, and for the same distance the low tide (V_0) and high tide volumes ($P_0 + V_0$) are recorded. This defines Section 0 through which there is no net exchange on the flooding tide. The next section is located at the point where the enclosed low tide volume ($V_0 + V_1$) has increased by a volume equal to the high tide volume ($V_0 + P_0$) of the previous segment. The low tide, high tide and tidal prism volumes at this point, read from the various curves, are recorded. This process is repeated, placing each successive boundary where the increase in the low tide volume equals the high tide volume within the adjacent landward segment. The lengths of the segments enclosed by successive boundaries give the average excursion of a particle of water on the flooding tide.

TABLE II. Segmentation of Raritan River and Bay, Using a River Flow of 33×10^6 Ft.^{3}/Tidal Cycle (740 Ft.^{3}/Sec.)

	Segment (n)	Distance from River Mouth, miles	Length of Segment, miles	Cumulative Volumes (10^6 ft.^{3}) Low Tide $\Sigma_0^n V$	Tidal Prism $\Sigma_0^n P$	High Tide $\Sigma_0^n (P + V)$
Raritan River	0	10.1	2.90	10	33	43
	I	7.8	2.30	53	75	128
	II	5.8	2.00	138	116	254
	III	4.1	1.70	264	180	444
	IV	2.2	1.90	454	305	759
	V	0.2	2.00	770	500	1,270
Raritan Bay	VI	1.1	1.30	1,280	800	2,080
	VII	2.2	1.10	2,090	1,190	3,280
	VIII	3.1	0.90	3,290	1,710	5,000
	IX	4.2	1.10	5,010	2,500	7,510
	X	5.5	1.30	7,520	3,500	11,020
	XI	7.1	1.60	11,030	4,960	15,990
	XII	8.3	1.20	16,000	6,600	22,600
	XIII	9.6	1.30	22,610	9,200	31,810

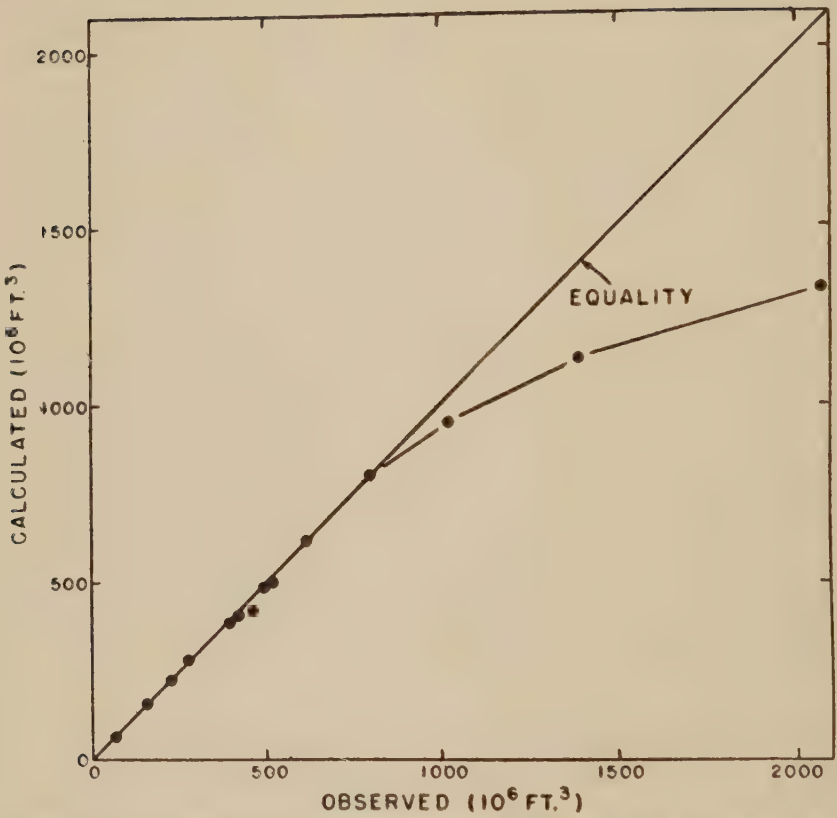

Figure 2. Comparison of the calculated accumulation of river water in Raritan River and Bay with the accumulation observed during a survey conducted in December 1948. The river flow was 33 x 10^6 ft.^{3}/tidal cycle (740 ft.^{3}/sec.).

The volumes within each segment, the tidal exchange ratios, and the calculated accumulation of river water are listed in Table III. The total volume of river water accumulated within the area has also been calculated from the salinity distribution observed during the hydrographic survey made in December 1948 (Ayers, Ketchum and Redfield, 1949). In Fig. 2 the accumulation of river water calculated by the theory described in this paper is compared to the accumulation observed during the survey. Excellent agreement between calculated and observed values was obtained within the eleven miles of the River and the first four miles of the Bay, where the total accumulated volume of river water was almost 800 million cubic feet. This volume of river water corresponds to 24 times the volume contributed by the river

TABLE III. Calculation of the Accumulation of River Water in Raritan River and Bay, Using a River Flow of 33 x 10^6 Ft.^{3}/Tidal Cycle (740 Ft.^{3}/Sec.)

Segment	*Length of Segment*	*Local Volumes*		*Exchange Ratio*	*Accumulation*	
		Intertidal P_n	*High Tide* $P_n + V_n$		Q_n	$\Sigma_0^n Q$
(*n*)	*miles*	10^6 *ft.*^{3}	10^6 *ft.*^{3}	*r*	10^6 *ft.*^{3}	10^6 *ft.*^{3}
0	2.90	33	43	0.767	43	43
I	2.30	42	85	0.494	67	110
II	2.00	41	126	0.325	102	212
III	1.70	64	190	0.337	98	310
IV	1.90	125	315	0.397	83	393
V	2.00	195	510	0.382	86	479
VI	1.30	300	810	0.370	89	568
VII	1.10	390	1200	0.325	102	670
VIII	0.90	520	1720	0.302	109	779
IX	1.10	790	2510	0.315	105	884
X	1.30	1000	3510	0.285	116	1000
XI	1.60	1460	4970	0.294	112	1112
XII	1.20	1640	6610	0.248	133	1245
XIII	1.30	2600	9210	0.282	117	1362

during a tidal cycle, i. e., to about the first 12 days of transport. Beyond this, the accumulation of river water calculated from the theory is less than the observed volumes of river water.

From the calculated accumulation of river water in each volume segment of the estuary, the percentage of fresh water and the salinity this would produce have been calculated. In Fig. 3 these are compared with the observed distribution of salinity and fresh water.[3] It will be seen that the difference between the calculated values and the observed values of accumulated river water in the outer part of the Bay correspond to small salinity differences. Since the plot in Fig. 2 is a cumulative one, and since the volumes in the Bay are great, this small difference in the salinity value results in a comparatively large discrepancy in the calculated total volumes. It is possible that the discrepancy is the result of incomplete horizontal mixing, the effects of which will be discussed below. The seepage of ground water into the Bay may contribute to the discrepancy.

It has been stated above that the subdivision of the estuary defines

[3] The source "sea water" which mixes with the Raritan River water is actually a mixture of Hudson River water and sea water which has a salinity of 27°/oo (cf. Ayers, Ketchum and Redfield, 1949). This is the reason the salinity approaches 27°/oo rather than a higher salinity as the percentage of Raritan River water approaches zero.

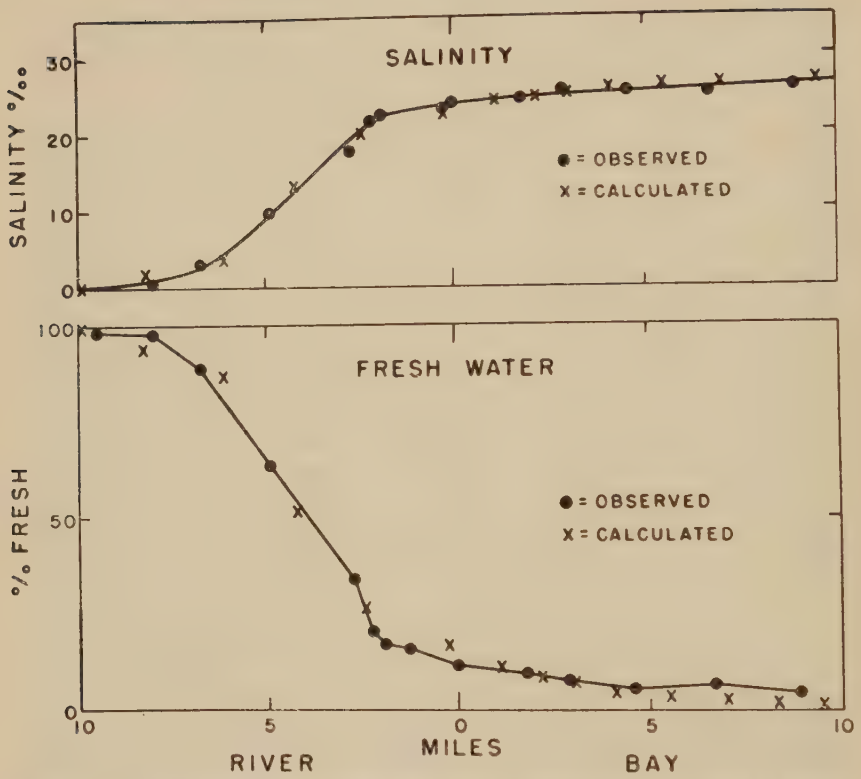

Figure 3. The observed and calculated distributions of salinity and fresh water in Raritan River and Bay in December 1948.

the average excursion of a particle of water on the flooding tide. A comparison of the distances between the boundaries in Table II with tidal currents measured by the Coast and Geodetic Survey (Marmer, 1935) is informative. Within the segments numbered X and XI, for example, the observed tidal currents at four stations at the center of the Bay produced transports which averaged 2.35 miles on the flooding tide.[4] The average velocity across the section would be approximately 0.7 of the velocity measured near the axis of the current. The average transport at this point would thus be about 1.65 miles per tide. The length of Segment X is 1.3 miles, of XI 1.6 miles. Measured currents at other locations within the Bay also gave trans-

[4] These transports are computed on the assumption that the tidal current curve approximates a cosin curve and that the average current velocity is $2/\pi$ multiplied by the maximum velocity.

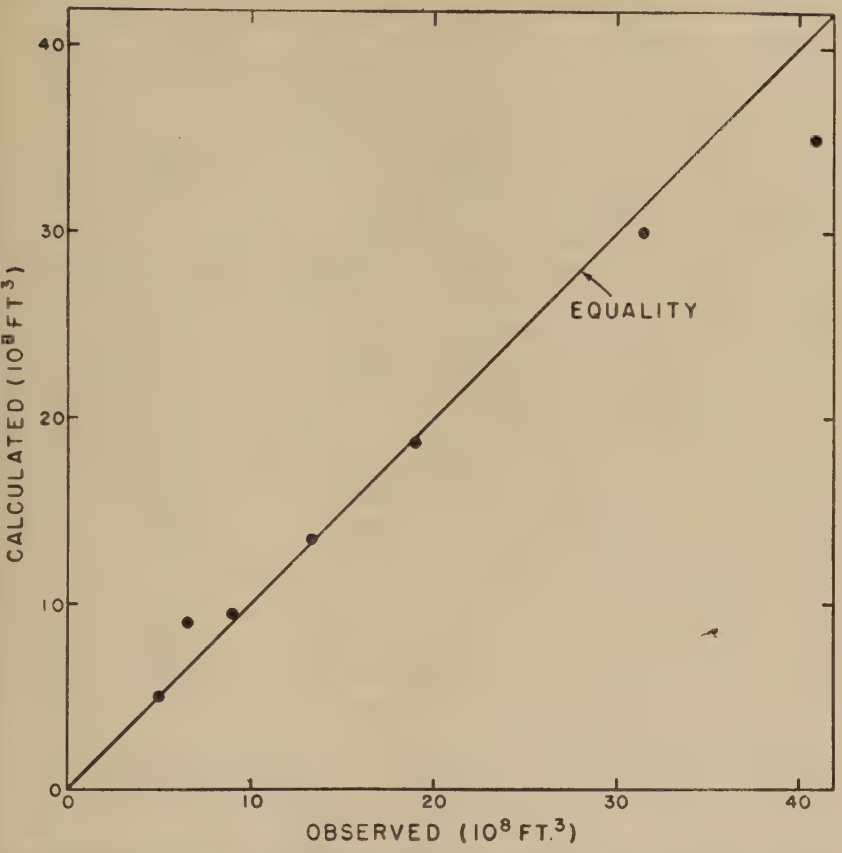

Figure 4. Comparison of the calculated accumulation of river water in Alberni Inlet with the accumulation observed by Tully (1949) on June 4, 1941 when the river flow was 1.2 x 10^8 ft.^{3}/tidal cycle (2,740 ft.^{3}/sec.).

ports which are approximately the same as the distances between boundaries calculated from the tidal displacement.

It may be concluded that the calculated distribution of fresh and salt water in Raritan River and Bay closely approximates the observed distribution for a length of about 15 miles of the estuary. The volume of river water within this part of the estuary corresponds to the volume introduced by the river during 24 tidal cycles.

Alberni Inlet, Vancouver Island, B. C. Tully (1949) has made extensive studies of the distribution of salinity and river water in Alberni Inlet. The Inlet is a typical fjord, having precipitous rocky sides with depths within the inlet as great as 1000 feet. This deep

water is separated from water at comparable depths in the Pacific Ocean by an outer sill at a depth of 120 feet. A length of more than 21 miles was surveyed, and the average width of the inlet over this distance was 1.2 miles. The total tidal prism for the surveyed area is about 40 x 10^8 cubic feet, which is approximately 30 times as great as the volume contributed by river flow during a tidal cycle at the time selected for comparison of results. In almost all respects, therefore, it is different from Raritan River and Bay.

Tully found that the river water was always limited in distribution to the upper 10 meters of water. The Inlet has therefore been subdivided into volume segments which consider only the upper 30 feet, and the exchange ratios have been computed accordingly. This treatment produces an average transport through the outermost section during the flood tide of 2.5 miles. The transport computed for the entire depth of water was only 0.15 miles. Although direct current measurements appear not to be available for comparison, Tully records float observations for the upper end of the estuary which indicate that the larger transport is more likely to be correct.

Tully, in his Table XIV, presents data showing the total accumulated river water at various times. On June 4, 1941, the data given for the two innermost stations were collected at high water, the next two stations were occupied on the ebbing tide, the outermost station on the flooding tide. These data are not strictly comparable, therefore, to the calculation of high tide distribution, but the inner end of the estuary, where variations with the stage of the tide would be greatest, was surveyed at the appropriate time.

Fig. 4 compares the accumulation of river water calculated from the tidal exchange theory with Tully's values for the accumulation. Except at the outer end of the estuary, where the calculated accumulation is too small, the agreement is reasonably good. The maximum accumulation corresponds to nearly 34 times the contribution from the river during a tidal cycle.

Great Pond, Falmouth, Mass. Great Pond is a narrow, sandy embayment on the south shore of Cape Cod which receives the outflow of the Coonamessett River. The Pond is about a mile and a half in length, averages less than a quarter of a mile in width, and has a maximum depth of 9 feet at high tide. The mean range of tide is about 1.5 feet. The tidal prism volume for the surveyed part of the pond is 7.6 x 10^6 cubic feet, which is about 15 times as great as the volume introduced by the river during a tidal cycle at the time of the survey.

A survey of this pond was made in June 1950 when the river flow was half a million cubic feet per tide (10.7 ft.^{3}/sec.). The

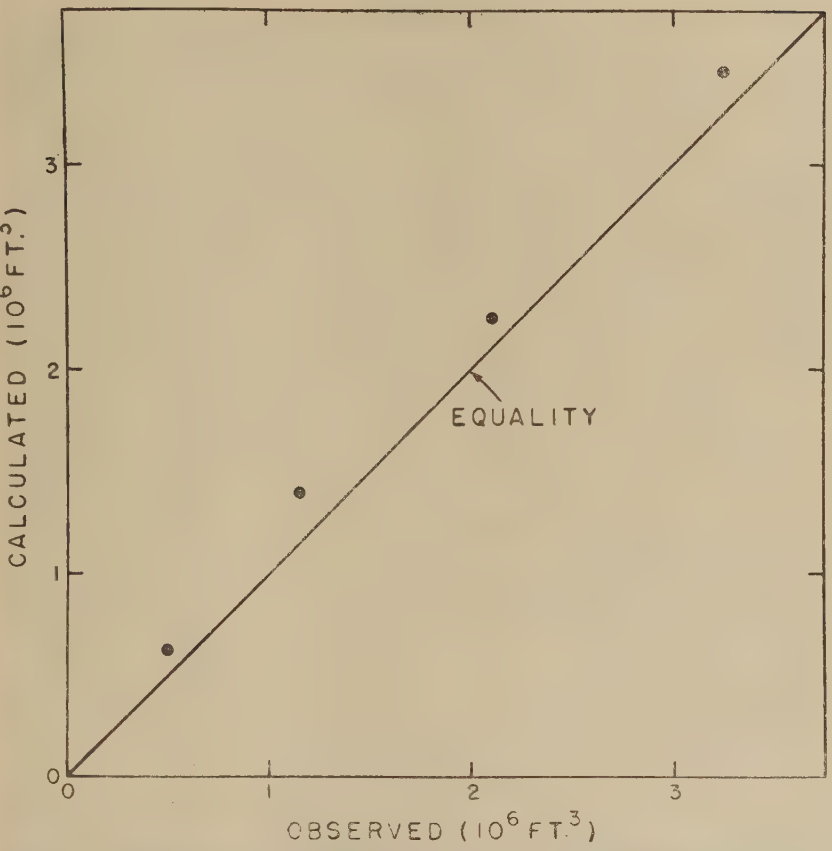

Figure 5. Comparison of the calculated accumulation of river water in Great Pond with the accumulation observed during a survey conducted on June 26, 1950 when the river flow was 0.5 x 10^6 ft.^{3}/tidal cycle (10.7 ft.^{3}/sec.).

salinity indicated that the river water was mainly restricted in depth to the upper half of the pond at high water. Consequently, in this pond, as in Alberni Inlet, the calculation must be made to the depth of the mixed layer in order to correct for incomplete vertical mixing.

The calculated volume of river water accumulated in the pond is compared to the volume deduced from the salinity distribution in Fig. 5. The agreement is good for the first mile of the estuary, which was as far as the calculation could be carried, since the next cross section would have been located beyond the limits covered by the survey. The total volume of accumulated river water was seven times as great as the volume contributed by the river during a tidal cycle.

DISCUSSION

It is somewhat surprising that a theory as simplified as this can be applied to such dissimilar estuaries as Raritan River and Bay, Alberni Inlet, and Great Pond. In order to illustrate the range of differences, some characteristics of the three estuaries are listed in Table IV. Perhaps one of the most interesting comparisons is between the volumes of the tidal prism and river flow, since these are the characteristics used in the calculations. There is more than a thousandfold range in the volume of the tidal prism and a range of 240 in the volume of river flow. The ratios between the tidal prism volume and river flow are also given in Table IV; they show that the tidal prism volumes vary from 15 to 279 times as great as the volume of river water contributed during a tidal cycle, an almost twentyfold range.

TABLE IV. Some Characteristics of the Three Estuaries Discussed

Characteristic	*Raritan River and Bay*	*Alberni Inlet*	*Great Pond*
Surveyed Length—Nautical miles	20	21	1.5
Surface Area—Sq. nautical miles	45	16	0.375
Maximum High Tide Depth—Feet	40	1000	9.0
Depth of Mixed Layer—Feet	Total*	30	3.5 – 5
Mean Range of Tides—Feet	5.5	6.4	1.5
Tidal Prism Volume (10^6 ft.^{3})	9200	4000	7.6
River Flow Per Tidal Cycle (10^6 ft.^{3})	33	120	0.5
Ratio $\frac{\text{Prism Volume}}{\text{River Flow}}$	279	33	15

* At each station the salinity was practically homogeneous from top to bottom. This survey was made in winter, and other observations show that stratification exists in summer.

The theory is based upon an assumption of complete mixing of water within various defined volume segments of the estuary at high tide. It will be useful to discuss, in a qualitative way, how incomplete mixing will influence the results of the calculation.

1. *Vertical Mixing.* The effects of incomplete vertical mixing have been discussed above but will be reviewed here. If the distribution of river water is restricted vertically to a surface layer, the actual tidal exchange will be greater than the exchange ratio calculated for the entire depth. A simple example will make this clear. If the mixed layer is half of the total depth at high tide, then the actual exchange will be $\frac{P}{0.5\,(P+V)}$. The exchange ratio (r) for half the depth would thus be twice as great as one calculated for the entire depth. The actual volume of river water accumulated within each segment (Q)

would be half of the volume which would be computed if the limitation of mixing to the upper half of the water column were ignored. This discrepancy can be corrected if salinity observations are available, and the correction has been used in both Alberni Inlet and in Great Pond.

2. *Transverse Horizontal Mixing.* It is frequently observed that the salinity contours in an estuary will indicate that, facing upstream, the salt water penetrates further on the right whereas the less saline water extends further seaward on the left of the estuary.[5] This is the result of the rotation of the earth. In such a distribution the mixing is obviously not complete in a transverse section across the estuary. A simple example will show the effect of this. If one postulates a distribution so that the estuary is divided into half longitudinally by the isohaline characteristic of pure sea water, one can assume that there is no seaward transport of river water through the right-hand half (facing upstream). Therefore all of the river water is escaping through the other half. The exchange ratio in this case would be $\frac{0.5\,P}{0.5\,(P+V)}$. The exchange ratio is thus the same as it would be for the entire segment and one would expect the same quantity of river water to accumulate. Since the river water would be contained in half of the total volume, however, it would obviously be present at twice the concentration.

3. *Longitudinal Horizontal Mixing.* If the mixing is not complete lengthwise between the sections defining the limits of a volume segment, the calculated exchange ratio will be too large and consequently the accumulation will be too small. If, for example, the mixing were complete over half, instead of over the total distance traversed by a particle of water during a flood tide, one should apply the same exchange ratio to two adjacent segments instead of to the single segment in order to compute the actual accumulation. The volume segment would thus contain double the accumulation calculated by the unmodified theory. It is possibly this error which results in the low calculated values at the outer ends of both Raritan Bay and Alberni Inlet. Unfortunately, there is no independent criterion which can be used to correct the exchange ratio for this condition. It can be recognized only by comparison of calculated with observed distributions.

The subdivision of the estuary is an integral and essential part of the theory. Sanitary engineers have considered the entire tidal prism

[5] This description applies to the northern hemisphere and would be reversed in the southern hemisphere.

at any cross section as though it were available for the dilution of introduced pollution. This inherently assumes that the mixing is complete longitudinally throughout the length of the estuary. Such a use of the tidal prism is an extreme example of incomplete longitudinal mixing. The above discussion shows that such an assumption will give too small an accumulation of river water, since a single exchange ratio is applied to the estuary as a unit. This leads to an exaggerated estimate of the rate of flushing. The application of the theory described in this paper to sanitary engineering problems is discussed by Ketchum (1951).

Two criteria are available to determine whether the tidal exchange theory will give valid estimates of the distribution of fresh and salt water within the estuary. Where current data are available, comparison of the average excursion per tide with measured tidal currents provides a valuable check on the definition of the volume segments. It should be remembered, however, that sufficient current data are rarely available to obtain an accurate average flow across the complete cross section. Approximations must be used, such as those described by Keulegan and Hall (1950), as was done in this paper for Raritan Bay. Absolute agreement cannot be expected.

The salinity data can be used to determine whether mixing is vertically complete or not, and if it is not complete the correction for vertical mixing can be applied. The comparison of average salinity at any cross section in the estuary with a plot of the calculated longitudinal distribution of salinity, such as that shown in Fig. 3, gives a check on the horizontal mixing anomaly for the part of the estuary where salinity data are available.

The value of the theory lies in the fact that it describes the exchanges throughout the estuary which are necessary to maintain the steady state distribution. This implies that the physical processes controlling the distribution are incorporated in the theory, though the individual effect of each process cannot yet be evaluated. The major practical advantage of the theory is that it permits calculation of the distribution of fresh water and salinity to be expected in any given estuary with a variety of river flows. The calculations can be made without undertaking field work, since existing data found in tide tables, water supply journals, and navigation charts are used. The validity of the calculated distribution can be checked by comparison with salinities at high tide at various points within the estuary.

The theory has been developed with river water as an indicator substance. It should be pointed out that the same exchange ratio will apply to anything suspended or dissolved in the water. Thus, for example, if one were interested in the distribution of plankton, fish

eggs, or pollution, the exchange ratio multiplied by the observed concentration would give a measure of the movements of the material to be expected during a tidal cycle. If, however, there is not a continuous and constant rate of supply of the material, the steady state conditions would not apply. If the rate of supply is known, however, the exchanges can be calculated and the distribution deduced as the tidal exchange distributes the material throughout the estuary.

SUMMARY

1. An empirical theory is presented which describes the exchanges between various parts of an estuary as a result of tidal oscillations and which permits the calculation of the average distribution of fresh and salt water within the estuary.

2. The characteristics of the estuary used in the calculation are the mean range of tides, the river flow, and the topography, all readily available for most estuaries.

3. The fundamental assumptions are: a) That a steady state distribution of fresh and salt water will exist throughout the estuary if the river flow is constant; b) that complete mixing will occur within volume segments defined horizontally by the width of the estuary and by the average excursion of a particle of water on the flood tide and vertically by the depth of the mixed layer. Discrepancies produced by incomplete mixing are discussed.

4. The calculated distributions of river water are compared with observed distributions for three very different estuaries, Raritan River and Bay, Alberni Inlet, and Great Pond. The tidal prism for these three estuaries includes more than a thousandfold range of volume, and the river flow varies by a factor of 240. The theory produces results which correspond closely with observed distributions of salinity and fresh water in all three estuaries.

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A FURTHER STUDY OF UPWELLING AND ASSOCIATED VEGETATION ALONG PACIFIC BAJA CALIFORNIA, MEXICO

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ABSTRACT

A temperature survey in the upper 200 feet of coastal waters of Baja California, from Bahía de Todos Santos to Bahía de la Magdalena, during the spring of 1950, has demonstrated the occurrence of upwelling along virtually the entire coast except within Bahía Viscaino and between Lat. 24° 50′ and 26° N. A study of the marine vegetation of this coast and of the outlying islands has shown close correlation with the presence or absence of upwelling water. Within the upwelling areas many genera and species indicative of cool northern waters occur far south of their expected latitudinal range. Such plants are for the most part lacking from the more tropical flora of Isla Guadalupe, which lies beyond the effects of coastal upwelling, while an intermediate flora, in composition much like that of La Jolla, California, occurs at Islas San Benito. Marine vegetation characteristics indicate that south of Lat. 27° N. a change in the pattern of summer winds must occur, causing upwelling to discontinue after spring with the consequent development of warm shore-water conditions.

INTRODUCTION

Seven years ago our knowledge of the distribution of marine algae along the Pacific Coast of Baja California amounted to records of few more than a score of species, most of these from the northernmost part of the peninsula. However, recent years have seen the accumulation of comprehensive collections[2] from virtually all parts of this coast, and an examination of these has brought to light numerous extensions of known ranges. These extensions of range in some species have revealed wide discontinuities in distribution, while in others they have indicated the occurrence of northern species far

[1] Contribution Number 56 from the Allan Hancock Foundation.

[2] Field work was begun independently by the writer in 1945 and was continued in 1946–47 with the support of a Guggenheim Fellowship. More recently, collections have been obtained on Allan Hancock Expeditions aboard the Velero IV. P. C. Silva has made collections at Islas San Benito and at Isla San Martín in 1950 during the Sefton Expedition. Incidental collections have been received from C. L. Hubbs, W. Williams, and B. F. Osorio Tafall.

south of their expected latitudinal range. These peculiarities of distribution in turn have called for oceanographic explanation, much of which has been found in a recognition of the occurrence of upwelling along this coast.

Upwelling of subsurface water along the coast of Baja California is the result of the movement of surface water away from the shore under the influence of the prevailing north and northwest winds. Even though the wind direction may be parallel to the shore, the wind current takes an offshore direction under the influence of the earth's rotation. The upwelling water does not originate from great depths but represents coastal bottom water from depths of only a few hundred feet.

Since its lower temperature permits greater solubility of gases, and since its history of movement along the bottom provides a greater nutrient content, upwelled water constitutes a particularly favorable medium for photosynthesis by marine plants and for their consequent luxuriant development. Accordingly, many of the larger and more massive algae of higher latitudes may be expected to extend far toward the tropics within regions of upwelling and to contribute to a richly developed flora. Conversely, tropical and subtropical species may be expected to be absent from such cold water areas except in favorably sheltered localities and to exhibit various distributional discontinuities. Seasonal variation in the occurrence or intensity of upwelling may be expected to result in seasonal differences in the composition of the flora of a given region and wholly to exclude species of limited tolerance. Thus, in order to correlate better our expanding knowledge of the marine flora of Baja California, it has become increasingly important that a clearer understanding be obtained of the distribution of upwelling areas and of the relative intensity and continuity of upwelling in various localities.

Despite emphasis in the present study on the relationship of upwelling water to the distribution of sessile marine algae, it should be pointed out that the occurrence of upwelling has far reaching general effects not only on the biota of the immediate marine environment but upon the geology of the sea floor and upon the climate, geology and biota of the adjacent land. Thus, to summarize some of the important known effects of upwelling water as discussed by Brongersma-Sanders (1948), we may list the following:

1. Nearly complete rainlessness of the coastal region with consequent sparsity of vegetation. 2. Moderate humidity with high frequency of fog. 3. Abundant phytoplankton production with consequent abundance of zooplankton, plankton feeders, fish, and fish feeders. 4. A large bird population and consequent accumulation of

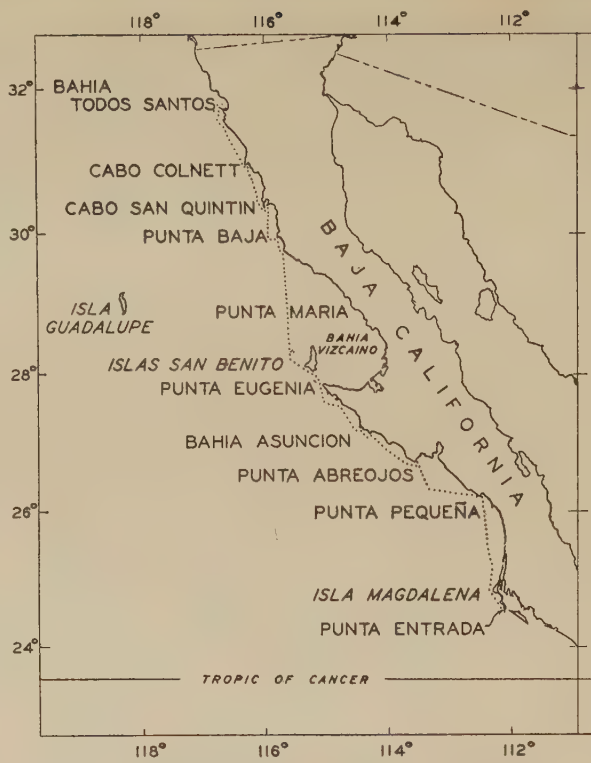

Figure 1. Chart of Baja California showing the course taken by the VELERO IV, April 24–May 1, 1950, in obtaining the temperature transection shown in Figs. 3–6.

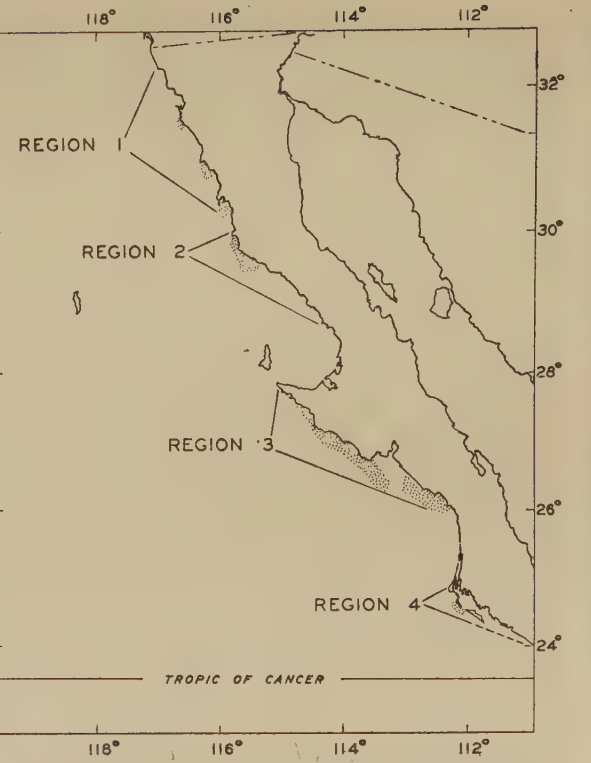

Figure 2. Chart of Baja California showing the four upwelling regions described in the text. The stippled areas represent localities in which water of less than 14° C was observed at the surface along the course shown in Fig. 1.

guano deposits on dry bird islands. 5. Periodic mass mortality of marine organisms from overdevelopment of noxious dinoflagellates (red water). 6. Deposition in the sea of sediments of high organic content. 7. Deposition on the land of sediments testifying of a very dry climate (wind-blown sand, salt).

With regard to these various effects of upwelling, the coast of Baja California shows remarkable similarity to the coasts of other major upwelling regions of the earth such as Chile-Peru, Southwest Africa, and Rio de Oro-Mauritania.

Along the northernmost part of Baja California, upwelling has definitely been recognized in several localities and has been correlated with the biota (McEwen, 1916; Dawson, 1946, 1949; Hubbs, 1948). Intensive studies of the inshore area between La Jolla, California and approximately Lat. 30° N. are now being carried on by C. L. Hubbs at Scripps Institution of Oceanography, and these studies promise to yield much information on the relation of upwelling to temperature conditions and animal distributions there.

South of Lat. 30° N. the occurrence of upwelling has been recognized in several localities between Punta Baja and Punta Santa Rosalia through the characteristics of the algal vegetation (Dawson, 1949); it has been measured hydrographically in the San Roque area (Dawson, 1950).

The present paper records the results of a continuous survey of the coastal waters from Bahía de Todos Santos to Bahía de la Magdalena (Fig. 1) between April 24 and May 1, 1950; they are accompanied by correlative collections of benthic algae and marine grasses at critical localities south of Lat. 30° N. The survey was made aboard the University of Southern California's marine laboratory ship VELERO IV under the command of Captain Allan Hancock whose many generosities are gratefully acknowledged. Surface temperatures were recorded continuously by means of a Brown potentiometer connected to a system of calibrated thermocouples, and 129 bathythermograms were obtained to depths of 200 feet with a standard surface-vessel bathythermograph. The positions of these BTs and their identifying numbers are indicated in the charts, Figs. 3–6.

The Spanish place names are given in accordance with the American Geographical Society's map of Hispanic America 1:1,000,000.

THE DISTRIBUTION OF UPWELLING

THE TEMPERATURE TRANSECTION, APRIL 24–MAY 1, 1950 (FIGS. 1, 3–6)

From inner Bahía de Todos Santos, where temperatures above 16° C occurred down to the bottom, rapidly decreasing temperatures were encountered as far as the channel between Islas de Todos Santos and

Punta Banda, where water of 13° occurred within 25 feet of the surface and appeared to represent a tongue of southward-moving upwelled water from the nearby Punta San Miguel-Punta Salsipuedes section of the coast. Southward to Lat. 31° 40′ N., at a point 6½ miles off shore, the 13° isotherm descended to 60 feet, this being accompanied by a comparable temperature increase at the surface, thus indicating pronounced dissipation of the upwelled water at this distance off shore.

At a point within one mile of shore on Lat. 31° 40′ N., the 13° isotherm again rose to within 35 feet of the surface, indicating moderate upwelling under the influence of Punta Banda headland. Passing coastwise to Lat. 31° 32′ N. off Soledad rocks, we observed 13° water at 65 feet and then at rapidly decreasing depths, so that it occurred almost on the surface one-half mile south of Punta Santo Tomás, where a small area of locally intense upwelling was indicated.

Southward toward Lat. 31° 23′ N., and seven miles off shore, steady dissipation of the upwelled water was observed as the 13° isotherm descended to 70 feet. Continuing coastwise at an average distance of eight miles off shore, we found 13° water paralleling the coast at a depth of about 70 feet, but upon nearing the shore again at Cabo Colnett a rapid decline in temperature at all depths accompanied the rise of the 12° isotherm to the surface in Bahía de Colnett. All observations in the Colnett area indicate that it represents a locality of intense upwelling during the spring and summer season. On April 25 the 13° isotherm remained within 25 feet of the surface for a distance of 15 miles to the south and 12 miles off shore at Arroyo Santo Domingo.

Observations continuing to a point two miles northwest of Cabo San Quintín identified the 13° isotherm at between 35 and 55 feet and gave indications of general dissipation of upwelled water under the influence of the north-south coastline south of Arroyo Santo Domingo. Upwelling was again evidenced south of Cabo San Quintín and throughout Bahía de San Quintín by a rise of the 13° and 12° isotherms to the surface.

The configuration of the coast south of Bahía de San Quintín suggests that upwelling should diminish southward to Punta Baja. This is substantiated by observations which indicate the rapid dissipation of upwelled water at Lat. 30° 15′ N. and the absence of appreciable renewal until Punta Baja is reached.

Latitude 29° 58′ N. at Punta Baja marks the northern boundary of an extensive area of upwelling along the entire southeasterly-trending coast to Bahía de Sebastian Viscaino. Recent observations have measured its occurrence only as far as Punta San Carlos, but studies of

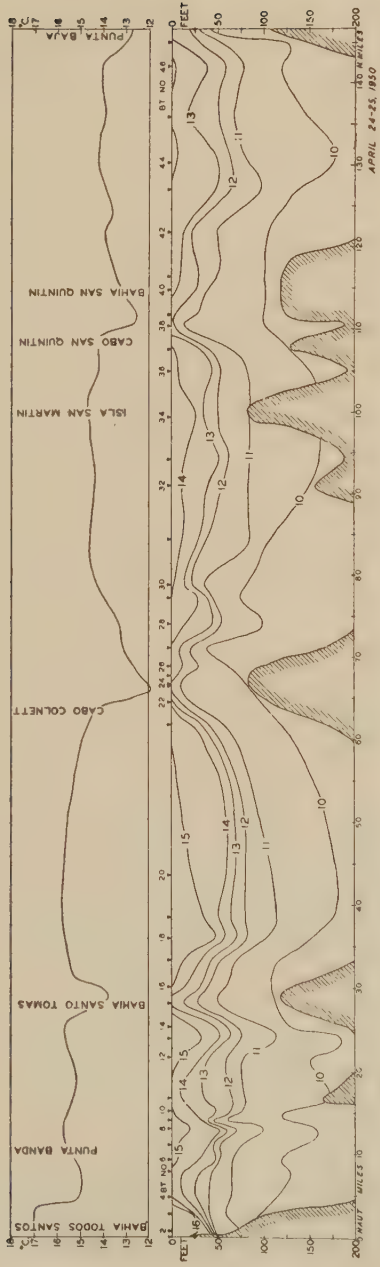

Figure 3. Surface temperature (above) and temperature transection (below) from Bahía Todos Santos to Punta Baja.

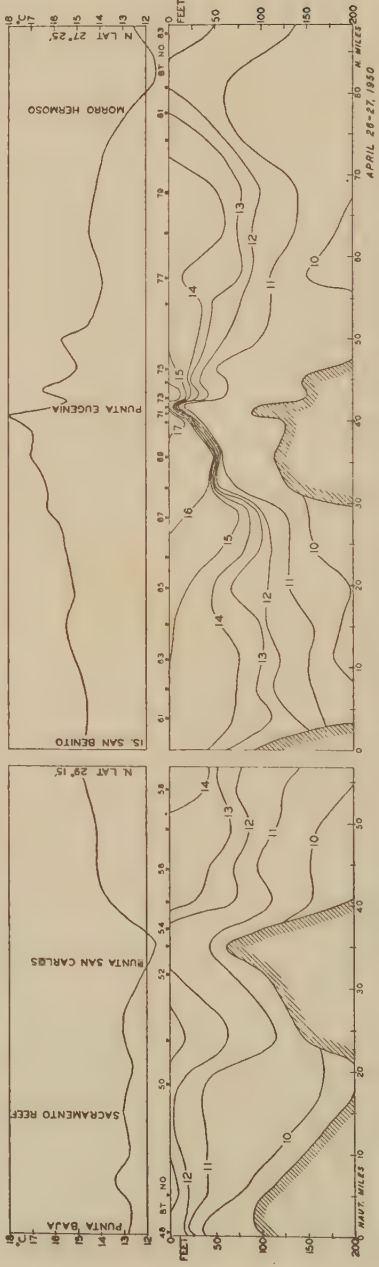

Figure 4. Surface temperature (above) and temperature transection (below) from Punta Baja to Lat. 27° 26′ N.

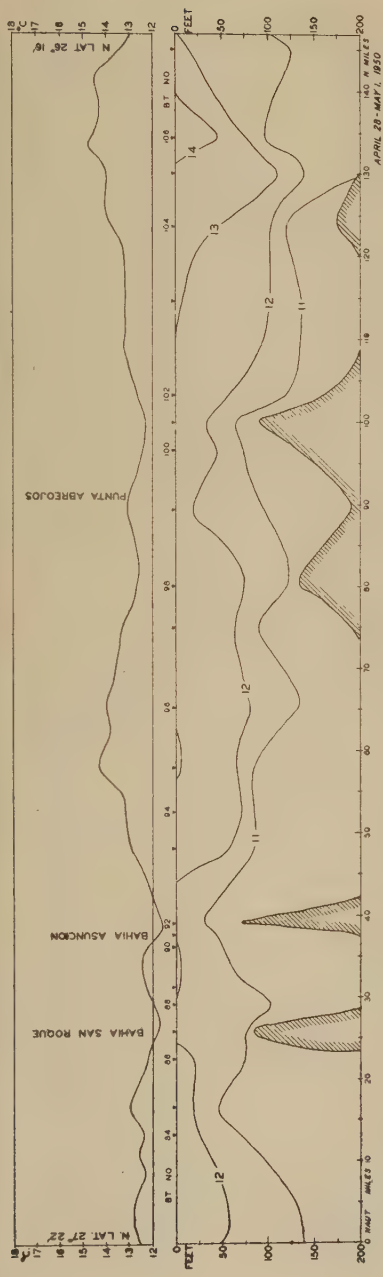

Figure 5. Surface temperature (above) and temperature transection (below) from Lat. 27° 22′ N. to Lat. 26° 16′ N.

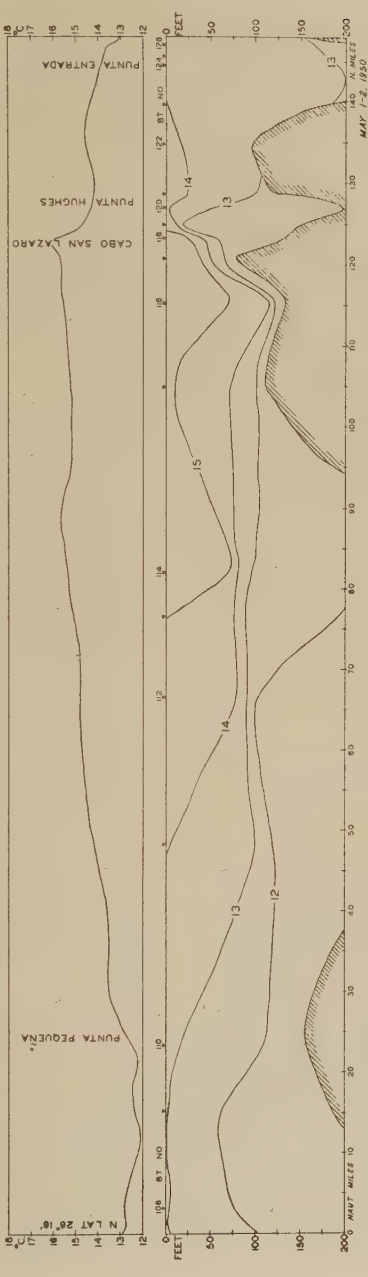

Figure 6. Surface temperature (above) and temperature transection (below) from Lat. 26° 16′ N. to Punta Entrada.

marine vegetation have already shown that the cold water influence extends to Punta María and affects algal growth and species distribution as far south as Punta Santa Rosalia. Continuing our observations coastwise from Punta Baja at distances of about six miles off shore, we recorded surface water temperatures at or below 13° to San Carlos anchorage, where a minimum of 11.6° was reached. This figure on April 26 represents the temperature of upwelling water after three days of light winds, force 1–3. On May 9, following ten days of strong winds, force 4-8, the surface temperature was 10.6° with equivalent temperature depression throughout the upwelling area.

Along the north–south transection from Punta San Carlos to Islas San Benito on April 27, the rise in temperature observed at all levels indicated a gradual dissipation of the effects of upwelling to a point about 45 miles off shore. Between Lat. 28° 35′ and 28° 45′ N., temperature maxima were recorded, but these were followed by a temperature depression again at all levels onward to Islas San Benito. The temperature pattern indicated by the observations on this course appears to agree with the expected movement of the upwelled water. Thus, the depressed temperatures in the Islas San Benito area seem to reflect the influence of upwelled water moving southwestward from the Punta Blanca-Punta María section of the coast just north of the Bahía de Viscaino eddy. On the other hand, the temperature maxima at Lat. 28° 45′ N. appear to represent a tongue of warmer offshore water moving in at this point to contribute to the divergence created by the Bahía de Viscaino eddy.[3] Despite the influence of this warmer offshore water, the effects of the upwelling water can clearly be seen in the character of the vegetation of Islas San Benito (see p. 51).

For 30 miles to the south and east of Islas San Benito, temperatures were observed to rise slowly until we reached the middle of Canal de Kellet, between Isla Cedros and Isla Natividad. There, at a depth of 50 feet, an abrupt 5° thermocline was encountered; this rapidly rose to 25 feet and then to 15 feet in Canal de Dewey. This prominent warm surface layer represents the southern outflow of highly insolated water from the southern margin of the Bahía de Viscaino eddy to which Laguna Ojo de Liebre (Scammon Lagoon) contributes. The prominence of this water, with temperatures above 16°, indicates the absence of upwelling along the southern coast of Bahía de Viscaino and the presence of warm marine conditions. Evidence obtained from the marine vegetation is in full support.

As we came abeam of Punta Eugenia a new region of upwelling was entered. The warm surface layer observed in the channels was quickly

[3] This pattern of movement seems to be identifiable in the chart of surface isotherms for August–September, 1908 presented by McEwen (1916).

dissipated and was no longer evident eight miles southwest of Punta Rompiente. In proceeding coastwise toward the southeast, the upwelling in this region intensified. Minimum temperatures were measured below Morro Hermoso, where the 12° isotherm reached the surface, and between Punta San Pablo and Bahía Asunción, where maximum upwelling intensity was indicated by temperatures as low as 11.5° at the surface.

Upwelling continued strong as far as Lat. 26° 30′ south of Punta Abreojos and Bahía de Ballenas where the 13° isotherm dropped appreciably below the surface for the first time south of Morro Hermoso. At this point the modifying effects of insolation on the large lagoon and estuary shoals of the region accounted for general temperature increases despite the apparent continuation of moderate upwelling to Punta Pequeña. The 13° isotherm reached the surface for the last time off Punta Santo Domingo, after which it was gradually depressed to about the 100 foot level, where it remained until Cabo San Lazaro was reached. The gradual and uniform rise in temperature at all depths along this southerly-trending coast pointed to a disappearance of upwelling between Punta Santo Domingo and Cabo San Lazaro.

Another region of upwelling was entered at a point 1½ miles off Cabo San Lazaro, where the 13° isotherm rose abruptly from a depth of 120 feet to 60 feet and then to 15 feet off Punta Hughes. The water throughout Bahía de Santa María and thence to the entrance of Bahía de la Magdalena continued isothermal down to the bottom at 14° or less, showing minimum temperatures about two miles southeast of Punta Entrada. Low water temperatures were observed for some distance inside Bahía de la Magdalena as a result of the tidal movement of upwelled water through the entrance.

The Upwelling Pattern

From data now at hand one may recognize four regions along Baja California that differ from each other according to the geographic and seasonal continuity of upwelling (Fig. 2). In the first of these regions, from Punta Descanso to Bahía de San Quintín, much of the coastline takes a nearly north-south direction, but it is broken by several headlands, south of which the coastline is at first east to west, then northwest to southeast. Since the winds are predominantly from the northwest in this region, upwelling is favored south of the headlands. That the areas of prominent upwelling are largely confined to the south sides of these headlands is shown by hydrographic observations (Fig. 3) as well as by the regular occurrence there of algal species characteristic of northern localities. The areas between the head-

lands show greater temperature variations, depending largely upon the degree of stagnation or movement of the cold upwelled water from the headlands. It is further evident from direct observation, as well as from a study of the vegetation, that where upwelling occurs in this region, particularly just below the headlands, it is continuous through the spring-summer season. Accordingly, there is exclusion from these "cold spots" of high temperatures resulting from insolation, such as may be of variable occurrence along the intermediate stretches of shore, particularly in Bahía de Todos Santos and Bahía de San Quintín.

A second region of upwelling appears to begin at Punta Baja, where an abrupt change in the trend of the coastline occurs and continues all the way to Bahía de Sebastian Viscaino. The east-west shore on the south side of Punta Baja provides for a local area of intense upwelling whose cold waters are augmented a few miles farther south by others along the continuous northwest-southeast coast from Punta San Fernando to Punta Santa Rosalia. Unlike the first region, the trend of the coastline here permits geographic continuity of upwelling. Although adequate information on wind direction is not readily available, it seems certain from indirect evidence that generally prevailing north and northwest winds continue to maintain the upwelling and consequent low temperatures through the summer season. McEwen's (1916) chart of surface isotherms for the summer of 1908 shows upwelling at Punta Baja and at Punta San Carlos. Furthermore, the characteristics of the vegetation along this coastal region seem to require this seasonal continuity of low temperature conditions. It is only in the extreme southern part of the region, at Punta Santa Rosalia and southward, that algal populations indicative of high summer temperatures are encountered and mark the end of upwelling coincident with the change in trend of the coastline.

The combined geographical and seasonal continuity of upwelling of the second region, coupled with the pattern of current movement required by the geography of Bahía Viscaino, permits the effects of this upwelling to be felt at a considerable distance seaward. The nearly closed pocket of Bahía Viscaino, open only by a 12 mile channel, partially blocks the normal southward flow of coastal waters and brings about a southwestward diversion of the upwelled waters of region 2, with the result that they move past Islas San Benito (see McEwen, 1916: pl. 9). As will be shown later, the cooling and nutrifying effects of this upwelled water are distinctly evident in the character of the flora of these islands.

The abrupt reversal in trend of the coast at Punta Eugenia initiates a third region of upwelling which extends without major geographic interruption all the way to Punta San Juanico, where the trend again

becomes north-south. The observations made in May indicate that upwelling is probably geographically continuous throughout this region, although in its southern part the temperature-raising effects of insolation on the surface water of shoals, of Laguna San Ignacio, and of other semi-enclosed lagoon areas, are clearly evident. A significant feature of this region is the restriction of a number of prominent algae indicative of cool water to the north of Bahía Asunción and the appearance in its southern part in spring of numerous evidences of the dominance of a warm water flora at a later season. These evidences, and the known occurrence of summer upwelling north of Lat. 27° N. (Dawson, 1950), suggest that this line is the approximate boundary of seasonally continuous upwelling, and that south of the above latitude a changing summer wind pattern is responsible for the confinement of upwelling to the winter-spring season.

The fourth region of upwelling has been investigated only between Cabo San Lazaro and Punta Entrada, but it probably extends along the easterly-trending coast approximately to Lat. 24° N. Although conclusive wind data are not available, evidence from the vegetation suggests that conditions favorable to upwelling cease at the end of the spring season, with the consequent development of higher summer temperatures and of a flora characteristic of them.

THE MARINE VEGETATION

Upwelling Region 1.

In connection with the recognition several years ago of cold water conditions south of the major headlands of northwestern Baja California, the writer has published elsewhere lists of some of the characteristic marine plants from this part of the coast (Dawson, 1946, 1949). Since the localities most favorable for the collection of marine algae are the extensive reefs of the headlands where maximum upwelling intensity occurs, most of the collections to date have emphasized the high proportion of species indicative of cold water conditions. They have shown in general a similarity to collections from the coast of California north of Lat. 34° N. and have consistently shown an absence of a number of indicator species characteristic of the warmer La Jolla area at Lat. 32° 50′ N. However, in keeping with the geographic discontinuity of upwelling in this region and the marked local variations in temperature depending upon the degree of stagnation or of movement of shore water, it should be noted that considerable local and seasonal variation in the vegetation occurs in this region. Moreover, two large areas occur upon which upwelling has little influence, namely, Bahía de Todos Santos and Laguna de San Quintín.

For a detailed account of the many interesting local and seasonal temperature variations in this region and the biological responses to them, we may look forward to the results of the thermal and zoological survey currently being carried out by C. L. Hubbs.

Upwelling Region 2.

Bahía del Rosario versus Isla Guadalupe. A comparison of the flora of Bahía del Rosario, characteristic of localities of maximum upwelling intensity in this region, with that of Isla Guadalupe, lying in almost the same latitude but beyond the effects of coastal upwelling, reveals marked differences which can be correlated with the hydrographic conditions of the respective stations. In a collection from Cañon Quemada on Bahía del Rosario, obtained in January 1950, all warm water elements such as *Sargassum*, *Zonaria*, *Dictyopteris*, *Halidrys*, *Dasya*, etc. were absent. The intertidal flora was dominated by a monotonous rock-cover association, mainly of *Gigartina serrata* and *Phyllospadix torreyi*. The only large and conspicuous intertidal brown algae were *Egregia laevigata* and *Pterygophora californica*, the latter being a plant unreported in intertidal habitats south of central California. Here *Pterygophora* seemed to take the place of the more southern *Eisenia arborea* which was absent. Several complanate species of *Gigartina*, such as *G. harveyana*, *G. volans*, *G. cristata*, and *G. californica* are pointedly characteristic of a cold water environment, as was also *Laminaria farlowii*. The absence of *Pterocladia pyramidale*, *Laurencia pacifica*, *Plocamium pacificum*, *Lithothrix aspergillum*, and other species normally to be expected in such a shore area contributed to the monotony in the flora. In all, only about 60 species were encountered in contrast to the more than 90 species collected at nearby Punta Baja headland, which is within range of somewhat warmer water counteracting the effect of upwelling. It may be conjectured that the reduced number of species in the Cañon Quemada locality is a reflection of both the intensity and constancy of upwelling, whereby the warming effect of insolation is so consistently reduced as to exclude a number of intertidal species which depend upon at least a limited season of higher temperature for the fulfilment of their reproductive functions.

In marked contrast with the flora of Bahía del Rosario is the flora of Isla Guadalupe, lying far to the west beyond the utmost reach of the effects of coastal upwelling. The waters bathing its shores, having traveled a long distance under conditions of increasing insolation and relatively slight mixing, are four to seven degrees higher in temperature than those along the peninsular coast. The result of this higher

temperature range is shown in the almost complete dissimilarity of the vegetation to that at Bahía del Rosario.

Of the following exemplary genera found at Bahía del Rosario and characteristic of cool waters along the Pacific Coast, only *Rhodoglossum* has been recognized in the writer's collections from Isla Guadalupe: *Pterygophora, Egregia, Laminaria, Schizymenia, Callophyllis, Gigartina* (complanate species), *Rhodoglossum, Gastroclonium, Ptilota, Cryptopleura, Nienburgia, Botryoglossum, Anisocladella, Microcladia.* On the other hand, of genera indicative of warm water, none of which occurred at Bahía del Rosario, the following are characteristic of Isla Guadalupe: *Cladophoropsis, Microdictyon, Padina, Dictyota, Dictyopteris, Colpomenia, Blossevillea* (*Cystophora*), *Sargassum, Liagora, Galaxaura, Asparagopsis, Gelidiella, Hypnea, Dasya, Spyridia.*

Islas San Benito versus La Jolla, California. The rather comprehensive collection of marine plants from Islas San Benito, obtained by the writer in April–May 1950, has proved to be a remarkable one in that it shows a striking similarity to the flora of La Jolla, California.[4] The explanation of this similarity seems to be found in the temperature conditions of the environment which are brought about by the combined effects of upwelling and of the associated current pattern of the region (see above). As data recently obtained would indicate, the result of this combination is the presence at these islands of warmer water than that upwelling along the peninsular coast but cooler than the offshore and long-insolated water of Isla Guadalupe. The thermal environment actually seems closely similar to that at La Jolla, 300 miles to the north, where diminished coastal upwelling combines with the presence of well insolated water from various offshore areas to bring temperatures to moderately high figures. In addition, the surf, exposure, and substrate characteristics are closely comparable in the two localities.

A majority of the more prominent species, most of which may be considered as indicators, have been identified from the recent collections (see Table I). Of 85 such species, about 82% are common to the floras of both La Jolla and Islas San Benito; about 7% occur only at La Jolla, and about 11% occur only at Islas San Benito. The large proportion of species common to both stations may be seen from Table I. Species characteristic of the Islas San Benito flora but absent from La Jolla are: *Bryopsis muscosa, Codium hubbsii, Padina durvillaei, Gloiopeltis minuta, Grateloupia howeii, Bossea angustata. Hypnea*

[4] This marked similarity to the La Jolla flora was also noted by P. C. Silva, who collected there during February of 1950 with the Sefton Expedition. I am grateful to him for several records listed in Table I.

TABLE 1. A List of Marine Plants Showing Their Occurrence or Absence at Each of Three Stations along Southern Baja California and at La Jolla, California

Species	*La Jolla, Calif.*	*Islas San Benito*	*Bahia Asunción*	*Isla Magdalena*
Phyllospadix scouleri Hooker	x	x	x	x
Phyllospadix torreyi S. Wats.	x	—	—	—
Chaetomorpha torta (Farl.) McClatch.	x	x	—	x
Chaetomorpha antennina Bory	x	—	—	x
Cladophora graminea Collins	x	x	—	—
Bryopsis corticulans Setch.	x	x	—	—
Bryopsis muscosa Lamx.	—	x	x	x
Codium fragile (Sur.) Hariot	x	x	x	—
Codium hubbsii Daws.	—	x	x	—
Ectocarpus variabilis (Saund.) G. M. Smith	—	—	x	—
Hapterophycus canaliculatus S. & G.	x	x	—	—
Sphacelaria furcigera Kütz.	x	—	—	x
Pachydictyon coriaceum (Holmes) Okam.	x	x	—	x
Dictyopteris zonarioides Farl.	x	x	—	x
Zonaria farlowii S. & G.	x	x	x	x
Taonia lennebackerae Farl.	x	x	x	—
Padina durvillaei Bory	—	x	x	x
Petrospongium rugosum (Okam.) S. & G.	x	x	x	—
Desmarestia munda S. & G.	x	x	x	—
Colpomenia sinuosa (Roth) Derb. & Sol.	x	x	x	x
Colpomenia ramosa Taylor	—	—	x	x
Scytosiphon bullosus Saund.	—	—	x	—
Scytosiphon lomentaria (Lyngb.) J. Ag.	x	x	—	—
Endarachne binghamiae J. Ag.	x	x	x	—
Macrocystis pyrifera (L.) Ag.	x	x	x	—
Pelagophycus porra (Leman) Setch.	x	x	—	—
Egregia laevigata Setch.	x	—	—	—
Eisenia arborea Aresch.	x	x	x	x
Pelvetia fastigiata (J. Ag.) DeToni	x	—	—	—
Hesperophycus harveyanus (Dec'ne) S. & G.	x	x	—	—
Halidrys dioica Gard.	x	x	—	—
Cystoseira osmundaceae (Menz.) Ag.	x	—	x	—
Sargassum palmeri Grun.	x	x	—	—
Sargassum agardhianum Farl.	x	x	—	—
Porphyra naiadum Anders.	x	x	x	—
Porphyra thuretii Setch. & Daws.	—	x	x	x
Erythrotrichia tetraseriata Gard.	—	—	—	x
Erythrotrichia porphyroides Gard.	—	x	x	—
Erythrotrichia pulvinata Gard.	x	x	x	—
Acrochaetium plumosum (Drew) G. M. Smith	—	—	x	—
Nemalion helminthoides (Velley) Batters	x	x	x	—
Gelidium cartilagineum var. *robustum* Gard.	x	x	x	x
Gelidium coulteri Harv.	x	x	x	x
Gelidium johnstonii S. & G.	—	—	—	x
Pterocladia pyramidale (Gard.) Daws.	x	x	—	x
Scinaia johnstoniae Setch.	x	—	—	x
Gloiopeltis minuta Kylin	—	x	—	—
Melobesia marginata Setch. & Fosl.	x	x	—	x
Melobesia mediocris (Fosl.) Setch. & Mason	x	x	x	x
Corallina officinalis var. *chilensis* (Dec'ne) Kütz.	x	x	x	x
Corallina gracilis Lamx.	x	x	—	—
Corallina vancouveriensis Yendo (varieties)	x	x	x	x

TABLE 1.—(*Continued*)

Species	*La Jolla, Calif.*	*Islas San Benito*	*Bahia Asunción*	*Isla Magdalena*
Bossea gardneri Manza	x	x	—	—
Bossea angustata Taylor	—	x	—	—
Lithothrix aspergillum J. E. Gray	x	x	x	x
Amphiroa peninsularis Taylor	x	x	x	x
Jania tenella Kütz.	x	x	—	—
Grateloupia howeii S. & G.	—	x	x	x
Grateloupia californica Kylin	x	—	—	x
Polyopes bushiae Farl.	x	x	x	—
Zanardinula kylinii Doty	x	—	x	—
Zanardinula filiformis var. *delicatula* Taylor	—	—	x	x
Callophyllis filicina Setch. & Swezy	x	x	—	—
Schizymenia pacifica Kylin	x	x	x	x
Hypnea johnstonii S. & G.	—	x	—	x
Plocamium pacificum Kylin	x	x	—	x
Plocamium violaceum Farl.	x	x	—	—
Gracilaria cunninghamii Farl.	x	x	—	—
Gracilaria cerrosiana Taylor	—	x	x	—
Gracilaria pachydermatica S. & G.	—	—	—	x
Ahnfeltia concinnna J. Ag.	—	—	x	x
Gigartina canaliculata Harv.	x	x	x	x
Gigartina leptorhynchos J. Ag.	x	—	—	—
Gigartina armata J. Ag.	x	—	—	—
Gigartina serrata Gard.	x	x	x	x
Rhodoglossum affine (Harv.) Kylin	x	x	x	—
Rhodymenia californica Kylin	x	x	x	x
Gastroclonium coulteri (Harv.) Kylin	x	x	x	—
Lomentaria catenata Harv.	—	—	—	x
Callithamnion rupicolum Anders.	x	x	—	x
Spermothamnion snyderae Farl.	x	x	x	—
Griffithsia pacifica Kylin	—	—	x	—
Ceramium codicola J. Ag.	x	x	—	—
Ceramium eatonianum (Farl.) DeToni	x	x	x	x
Ceramium taylorii Daws.	x	x	x	x
Ceramium californicum J. Ag.	x	—	—	x
Centroceras clavulatum (Ag.) Mont.	x	x	x	x
Nienburgia andersoniana (J. Ag.) Kylin	x	x	—	x
Anisocladella pacifica Kylin	—	—	x	—
Sorella pinnata Hollenb.	x	x	—	—
Myriogramme hollenbergii Kylin	—	—	—	x
Cryptopleura crispa Kylin	x	x	x	x
Pogonophora californica J. Ag.	x	—	x	—
Dasya californica Gard.	x	—	—	x
Heterosiphonia erecta Gard., em. S. & G.	x	x	—	x
Pterosiphonia dendroidea (Mont.) Falk.	x	x	x	x
Pterosiphonia baileyi (Harv.) Falk.	x	x	—	—
Polysiphonia collinsii Hollenb.	x	x	x	—
Polysiphonia hendryi Gard.	x	x	—	—
Polysiphonia johnstonii S. & G.	—	—	—	x
Polysiphonia concinna Hollenb.	x	—	x	—
Polysiphonia simplex Hollenb.	x	—	x	—
Pterochondria pygmaea (Setch.) Hollenb.	x	—	x	—
Herposiphonia parva Hollenb.	x	x	—	—
Lophosiphonia villum (J. Ag.) S. & G.	x	x	—	x
Laurencia pacifica Kylin	x	x	x	x
Laurencia scrippsensis Daws.	x	x	x	x

TABLE 1.—(*Continued*)

Species	*La Jolla, Calif.*	*Islas San Benito*	*Bahia Asunción*	*Isla Magdalena*
Laurencia snyderae Daws.	x	x	—	—
Chondria nidifica Harv.	x	x	x	—
Chondria californica (Collins) Kylin	x	x	x	—

johnstonii, Gracilaria cerrosiana. Species characteristic of the flora of La Jolla but conspicuously absent from the Islas San Benito intertidal flora as examined in April–May 1950 are: *Phyllospadix torreyi, Egregia laevigata, Pelvetia fastigiata, Gigartina leptorhynchos, G. armata, Zanardinula kylinii.*

Bahía Sebastian Viscaino. Field and laboratory studies of algae from the shores of Bahía Viscaino have shown (Dawson, 1949) that the marine flora of the eastern arc of the bay, between Punta María and Embarcadero de Miller, changes quite suddenly from a flora characteristic of cool waters, reflecting the marked influence of upwelling at Punta María, to one characteristic of warm semitropical waters, reflecting the disappearance of upwelling and the dissipation of the cooler upwelled water from the north as it moves southward and westward into the eddy. Although hydrographic observations within Bahía Viscaino were not included in the recently completed survey, the configuration of the coast and the temperature records obtained between Isla Cedros and Punta Eugenia (see p. 46) indicate that upwelling must be absent along this south-to-west arc, insolation high, and downward mixing slight. These conditions are required to account for the relatively high temperatures in the water flowing out through Kellet and Dewey channels. The vast shallow expanse of Laguna Ojos Liebre (Scammon Lagoon) contributes appreciably to the warming influence that gives the waters bathing this shore a tropical character. Only limited algal collections have been obtained thus far from this region, but in no instance do they fail to reflect warm water conditions. A few of the characteristic representatives indicative of a high temperature environment are: *Ruppia maritima, Valoniopsis pachynema, Sphacelaria hancockii, Padina durvillaei, Hydroclathrus clathratus, Colpomenia sinuosa* f. *tuberculata, Scinaia johnstoniae, Ceramium affine* var. *peninsularis, C. clarionensis, C. fimbriatum, Griffithsia multiramosa, G. tenuis, Spyridia filamentosa.* Undetermined fragments of *Hypnea, Liagora* and *Dasya* also occur and are in keeping with the character of the warm water flora.

Upwelling Region 3.

The effects of a transition to seasonal discontinuity of upwelling and of temperature-modifying geographical conditions on the marine

vegetation of this region may best be recognized by considering four localities in turn, namely, Bahía de Asunción, Punta Abreojos, Laguna de San Ignacio and Punta Pequeña.

In Bahía de Asunción, approximately in the center of this third region of upwelling, minimum temperatures characteristic of the entire region have been found during both spring and summer. The flora of Bahía de Asunción, which may be considered representative of the northern half of region 3, shows some points of contrast with that of region 2 to the north. Although the presence in May of luxuriant growth and of a conspicuous predominance of species indicative of cool water gave evidence of the marked effect of upwelling on the flora, the absence of several other northern species and the presence of an admixture of warm water elements indicated that the effects of upwelling are probably not so strongly pronounced throughout the year. The absence of *Pelvetia* and *Hesperophycus* from the upper zone, and the occurrence of *Padina*, *Amphiroa* and luxuriant *Colpomenia* in tide pools, pointed respectively to the dessicating and warming effects of the intense insolation of the desert coast on the flora. The vegetation of protected local areas resembled that at Punta Santa Rosalia, where the flora of upwelling region 2 grades into the warm arc of Bahía Viscaino. At low levels on the open headland, in shaded crannies and under the protection of the abundant *Phyllospadix*, the more northern cool-water species were to be found for the most part, but in situations exposed to the direct heat of the sun and to dessication of the air, a marked decrease in the frequency of northern types was evident. The complete absence of such cool-water indicators as the complanate gigartinas (even from sublittoral drift) and of the non-complanate ones (except for *G. canaliculata*) seems to reflect a decline in upwelling intensity in summer. On the other hand, the presence of luxuriant beds of *Macrocystis* indicates that upwelling is still essentially continuous this far south in region 3.

Some of the larger species known from region 2, whose absence from the Bahía de Asunción station seems indicative of declining upwelling intensity during summer, with resultant prohibitively high temperatures, are: *Egregia laevigata*, *Gelidium nudifrons*, *Zanardinula andersoniana*, *Gymnogongrus platyphyllus*, *Gigartina leptorhynchos*, *G. harveyana*, *G. californica*, *G. volans*, *Rhodoglossum americanum*, *Cryptopleura violacea*, *Microcladia coulteri*.

Although extensive beds of the perennial *Macrocystis* occurred throughout the Isla San Roque-Asunción area, these were no longer observed at Punta Abreojos. Their absence there appears to reflect regular seasonal discontinuity of upwelling and normal development of high shore-water temperatures in summer. Much of the vegetation

observed on April 30, 1950 on the open west and south exposures of the headland was like that at Bahía de Asunción, although more marked dwarfing of such plants as *Gigartina canaliculata* was apparent. Immediately to the east, however, a more sheltered reef area is subject to diminished surf and increased insolation at low water, with the result that tropical conditions are more distinctly evidenced than anywhere at Bahía de Asunción. The tropical echinoderms *Heliaster microbrachiatus* and *Echinaster tenuispinus* occurred there in pools occupied by *Amphiroa* and *Padina,* while the rock cover consisted mainly of a dense, depauperate, broad-bladed form of *Gelidium coulteri* and dwarfed *Corallina vancouveriensis.* The absence of *Sargassum,* as was also noticed at Bahía de Asunción, suggests that the range of the more northern *S. agardhianum* had been passed over and that the range of the tropical annual sargassums was being reached. Fragments of *Sargassum,* apparently of the *S. sinicola* complex, in high and dry drift, supported this assumption, as did the presence of abundant juvenile *Sargassum* at Bahía de la Magdalena to the south. These indications are in agreement with the report (Dawson, 1949) that *Sargassum* along the tropical Mexican Coast is almost entirely of summer development, being absent or scarcely evident in winter and early spring.

Of infratidal species indicative of increasingly warm conditions, there were the following: *Sporochnus pedunculatus, Scinaia johnstoniae, S. latifrons,* and *Dasya pedicellata.*

To the east of Punta Abreojos, across Bahía de Ballenas, the effective lowering of shore-water temperatures by upwelling is appreciably reduced due to shoaling and the occurrence of numerous estuaries and lagoons. The largest of these, Laguna de San Ignacio, provides a great expanse of quiet shallow water that is exposed to the intense heat of the tropical sun. The flora of the lagoon characteristically consists of strictly heat-loving species adapted to an environment of slight agitation and of low carbon dioxide, oxygen and nutrients. Some of the exemplary inhabitants of the lagoon are the following, collected in February 1950 by C. L. Hubbs, M. W. Johnson and A. A. Allanson of Scripps Institution of Oceanography: *Colpomenia sinuosa* (several forms), *Hydroclathrus clathratus, Scinaia johnstoniae, Amphiroa annulata, Jania capillacea, Hypnea* sp., *Lomentaria hakodatensis, Dasya pedicellata, Griffithsia multiramosa, Hypoglossum attenuatum, Polysiphonia concinna, P. snyderae.*

The headland of Punta Pequeña, guarding Bahía de San Juanico, is situated in the southern extremity of the third region of upwelling. Although upwelling may occur moderately in this area for a considerable winter-spring period and may provide an ample supply of nu-

trients from the great expanse of shoals to the south and west, it is clear from temperature measurements and from the characteristics of the vegetation that temperatures generally are modified upwards by the lagoons to the north and by the shoals and that summer and fall water conditions must become comparatively warm. The absence of the perennial *Macrocystis* is in accord with the latter, and the absence or dwarfed character of various northern species reflects the former. The reason for the occurrence of large quantities of *Desmarestia munda* in drift from the infratidal zone is not understood, although a modification of the species for higher temperatures is recognizable in the distinct narrowing of the blades.

Upwelling Region 4.

From Punta Pequeña and Punta San Juanico the coast of Baja California consists of a great southward sweeping sandy beach broken only by occasional estuary and lagoon entrances. No rocky shore occurs until the shoulder of a volcanic cone interrupts the sand at Cabo San Lazaro. Apparently, upwelling is absent all along this sandy arc, and insolation normally brings about steadily rising temperatures. In the spring, immediately opposite Cabo San Lazaro, one encounters a new region of cold water that supports a flora consisting largely of northern elements but in which the relative dominance of the northern elements is decidedly less than at Bahía de Asunción. Although the largest and most conspicuous intertidal brown alga (as observed in March and May) was *Eisenia arborea*, the abundance of juvenile *Sargassum* indicated a shift to dominance of that genus at a later season. The beds of *Macrocystis* were absent. Although fresh fragments in drift (if actually of local origin) suggested that a limited amount of this plant may occur off shore, it does not appear in sufficient quantity or size to be visible at the surface. The long quoted hearsay of fishermen (Setchell and Gardner, 1925) to the effect that "these beds extend to Magdalena Bay" is not altogether true. Furthermore, a notable assemblage of species characteristic of the Gulf of California becomes evident there, all of which represent extensions of known ranges along the Pacific peninsular coast: *Gelidium johnstonii, Grateloupia howeii, Hypnea johnstonii, Gracilaria pachydermatica, Lomentaria catenata, Polysiphonia johnstonii.*

SUMMARY

Combined biological and hydrographic investigations of the coastal waters of Pacific Baja California have indicated the occurrence of extensive upwelling along much of this coast. Four regions can be

identified by differences in geographical or seasonal continuity of upwelling. The first of these regions has geographically discontinuous upwelling in which the centers of intensity are located on the south sides of the more prominent headlands. Local areas occur south of Punta Santo Tomás, Cabo Colnett, and Punta San Quintín, in which the high intensity prevents summer insolation from causing marked inshore temperature increases. The second region is evidently geographically and seasonally continuous. Its algal flora, including *Macrocystis* and complanate gigartinas, indicates the continuation of low shore-water temperatures through the summer. Its influence is felt as far southwest as Islas San Benito, where a flora in composition very much like that of La Jolla, California reflects both the cooling and nutritional advantages of the upwelled water and the presence of moderate temperature increases in summer. In the third region, upwelling is probably geographically continuous, although the characteristic low surface temperatures are in part modified upwards by the effects of insolation on extensive shoals. The exclusion from this region of several northern indicator species and the limitation of *Macrocystis* north of Lat. 27° N. suggest that a transition in the seasonal wind pattern occurs in these latitudes. As a result the cooling influence of upwelling extends through the summer season north of Lat. 27° N., but to the south it discontinues after spring to allow summer temperatures to rise sharply. In the fourth region vegetation characteristics show that upwelling is confined to the winter-spring season.

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GROWTH AND SETTING OF LARVAE OF *VENUS MERCENARIA* IN RELATION TO TEMPERATURE

By

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ABSTRACT

Larvae of the hard shell clam, *Venus mercenaria*, were grown to metamorphosis at constant temperatures of 30.0, 27.0, 24.0, 21.0 and 18.0° C ± 1.0° C. The rate of growth of the larvae was generally, but not always, more rapid at high than at low temperatures. Within this range small differences in temperature, such as 1.0 or 2.0°, were not extremely important in affecting the rate of growth. The average time needed by larvae to reach a certain size or to grow to metamorphosis at different temperatures is given. Larvae obtained from the same sources and grown under identical conditions often showed considerable individual variations in the rate of growth and in the time needed to reach the stage of metamorphosis. Fertilized eggs placed in water of 15.0 or 33.0° C ± 1.0° C showed abnormal development and heavy mortality, few ever reaching veliger stage. Some food requirements of the larvae are discussed.

INTRODUCTION

At some time or other almost every student of ecology or physiology of larvae of lamellibranch mollusks has commented that temperature is the factor influencing the duration of their pelagic life. Unfortunately, most of these comments were usually too brief and incomplete. Others, even if lengthy, lacked supporting data to be of much value in analyzing the relationship between temperature and growth of larvae.

Since a review of the literature devoted to the effects of temperature upon larvae of lamellibranchs has recently been offered by Thorson (1946) and Baughman (1947), there is no need to repeat it here. We shall merely mention a few articles that have a close relation to our studies. Nelson (1908) stated that within the temperature range from 24.0 to 27.0° C the American oyster, *Ostrea virginica*, has a free-swimming period of only one week. At 23.0° C, however, this period is extended to 13 days, and at 20.0° C to 17 days. Medcof (1939) concluded that oyster larvae require approximately 24, 26 and 30 days to reach maturity at a constant temperature of 21.0, 20.0 and 19.0° C respectively. According to Korringa (1941), *Ostrea edulis* of Holland has a pelagic life of six days at a temperature of 22.0–23.0° C, 9 to 10 days at 18.0–21.0° C, and 13 to 14 days at 16.0–17.0° C. Belding (1912) thought that the free-swimming period of larvae of *Venus*

mercenaria is 10 to 12 days at a temperature of approximately 22.0° C, but somewhat longer at lower temperatures.

Thus, the general opinion is that temperature may hasten or prolong the larval period. Furthermore, it is believed that a difference of only one degree, between 19.0 and 20.0° C, may prolong the swimming period of larvae by as much as four days (Medcof, 1939). However, the accuracy of the day-degree relationships offered may be questioned, since the number of days needed by larvae of different lamellibranchs to reach the setting stage at certain temperatures was decided largely upon the basis of field observations, where it is always difficult and usually impossible to evaluate the relative importance of other factors such as salinity, pH, food, etc. It is thought, therefore, that such relationships can be best determined by laboratory experiments where most of the factors can be rigidly controlled. This paper offers a description of studies devised to determine the rate of growth, length of free-swimming period, and other aspects of the behavior of larvae of the hard shell clam, *Venus mercenaria* L., grown at different but constant temperatures.

We wish to express our appreciation to our colleague, John H. Peterson, for tabulating some of the data on which this article is based.

METHODS

The larvae were grown at constant temperatures of 33.0, 30.0, 27.0, 24.0, 21.0, 18.0 and 15.0° C ± 1.0° C. They were kept in earthenware crocks of 20-liter capacity. These crocks, which were covered with black painted glass to exclude the light, were immersed in large containers through which water of a constant temperature was running continuously, thus maintaining a constant temperature within the crocks. Duplicate crocks were used for each temperature. The crocks were filled with sea water filtered through a thick layer of cotton.

The largest part of this work was done during the winter and early spring, the time which we found most convenient to control the temperature of the water (Loosanoff, 1949). Sperm and eggs were taken from clams which were conditioned to spawn in winter (Loosanoff and Davis, 1950). To avoid the shock of temperature changes, the fertilized eggs were gradually brought up or lowered to the temperatures in which they were to be cultured. Usually one million eggs were introduced in each crock, making the initial concentration of 50,000 eggs per liter of water.

The cultures were changed every two days by using the method already described (Loosanoff and Davis, 1950). After the water had been changed, the larvae were fed a mixture of *Chlorella* sp. and a

purple sulfur bacteria, *Chromatium perty*, creating in the culture crocks a concentration of approximately 300,000 cells of *Chlorella* and 400,000 cells of sulfur bacteria per cc of water. It is interesting that the sulfur bacteria, which were rejected as food by the oysters (Loosanoff, 1949a), were readily taken in and apparently assimilated by the larvae of *V. mercenaria*.

Altogether four major experiments were conducted. In the first, no larvae were measured until the fourth day. In the subsequent experiments, however, larvae from all the cultures were measured at the end of the second day after fertilization. In one 30.0° C culture, measurements were made as soon as the larvae reached the straight hinge stage, which occurred in less than 24 hours.

From each crock 50 larvae were taken for measurement on each occasion. However, because the cultures were run in duplicate, the number of larvae taken as a sample for each temperature group was actually 100. As a rule, in all experiments the duplicate samples showed extremely close agreement.

Measurements of the larvae were made in the usual manner, using a Sedgwick-Rafter cell to hold the larvae. Since each of the small divisions of our ocular micrometer was equal to seven microns, most of our figures were based on these intervals. In some cases, when the necessity arose to determine the measurements more precisely, the larvae were measured under high-dry power where each division of the ocular micrometer was equal to only 1.7 microns. In general, however, it was found impractical to be confined to such accurate measurements, because the variation in the measurements of the larvae depended to some extent upon the position in which the larva was lying on the slide. This was especially true of the older larvae, the shapes of which were more rounded than those of the relatively flat young ones.

RESULTS

We would like to mention here that this discussion is based on the results of experiments in which the clams of only one geographic area—Long Island Sound—were used to furnish the spawn. This point is emphasized because it is considered possible that within the general population of *Venus mercenaria*, which extends from the Gulf of St. Lawrence to Texas, there are local races of clams whose physiological requirements may differ from those of Long Island Sound clams. That such physiologically-different races of the same genus may exist among lamellibranchs has been shown recently for the common American oyster, *Ostrea virginica* Gmelin (Loosanoff, unpublished manuscript).

First our discussion will be confined to the temperatures within the range of 18.0 to 30.0° C. The results observed at 15.0 and 33.0° C will be discussed later, because the development of the eggs and larvae at these temperatures was usually abnormal.

Within the range from 18.0 to 30.0° C the mortality of the eggs and then the larvae was comparatively low. It is estimated that often not less than 85% of these were carried to the stage of metamorphosis. The only exceptions were several cultures grown at 18.0° C, where somewhat fewer eggs developed into larvae of straight hinge stage. However, those that reached that stage usually lived through metamorphosis.

The larvae in all cultures behaved normally. They were usually vigorous and rapid swimmers, this condition necessitating that they be killed with formalin before measurements were taken. Their color was usually pinkish-yellow-green, characteristic of the type of food they were fed. Incidentally, our experience has shown conclusively that the color of larvae of *V. mercenaria*, as well as that of larvae of some other lamellibranchs, such as *Mya arenaria* and *Mactra solidissima*, with which we worked at different times, should not be considered as a reliable specific characteristic that may be helpful in identifying larvae. We formed this conclusion because we found that the color of the larvae may be changed at will, within an hour or so, by feeding them micro-organisms of different colors.

The data on growth of larvae at different temperatures in Experiments 1 through 4 are given in Figs. 1, 2, 3 and 4. The curves of these figures are based upon the mean length of the larval populations as determined by measurements of representative samples at two-day intervals. As already mentioned, the exception was Experiment 1, where the larvae were not measured until the end of the fourth day. In Experiment 4, which was conducted in the early summer when the water temperature was already higher than 18.0° C, no cultures were grown at that temperature. In Figs. 1, 2, 3 and 4 the curves terminate at 185 microns. This arbitrary size was taken as the terminal point of the curves because in some instances it was found that, when the mean length of the larvae in the culture was approaching 185 μ, many larvae were already metamorphosing, thus dropping out of the free-swimming population.

The metamorphosis of a larva of *V. mercenaria* into a young clam is not as sharply defined as is the metamorphosis or, as it is commonly called, setting of an oyster, at which time the larva ceases crawling entirely and cements itself to a shell or other clean object. In *V. mercenaria*, as well as in some other clams, metamorphosis is an extended process beginning with the gradual replacement of a ciliated

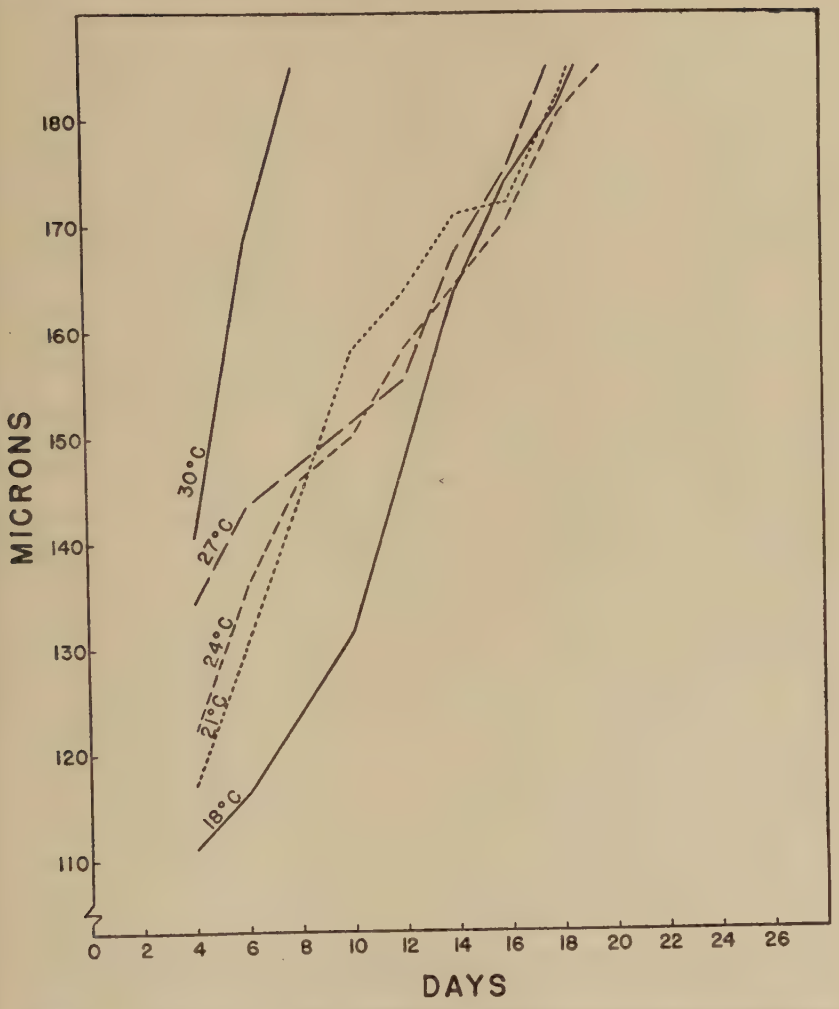

Figure 1. Mean length of larvae of different ages grown at five constant temperatures. Experiment 1.

velum with a large muscular foot and ending with the development in the foot of a functional byssal gland. This point is often difficult to establish, because many young clams, although possessing a byssus gland, do not always attach. Therefore, it may be difficult at times to distinguish a very young clam from an old ready-to-metamorphose larva.

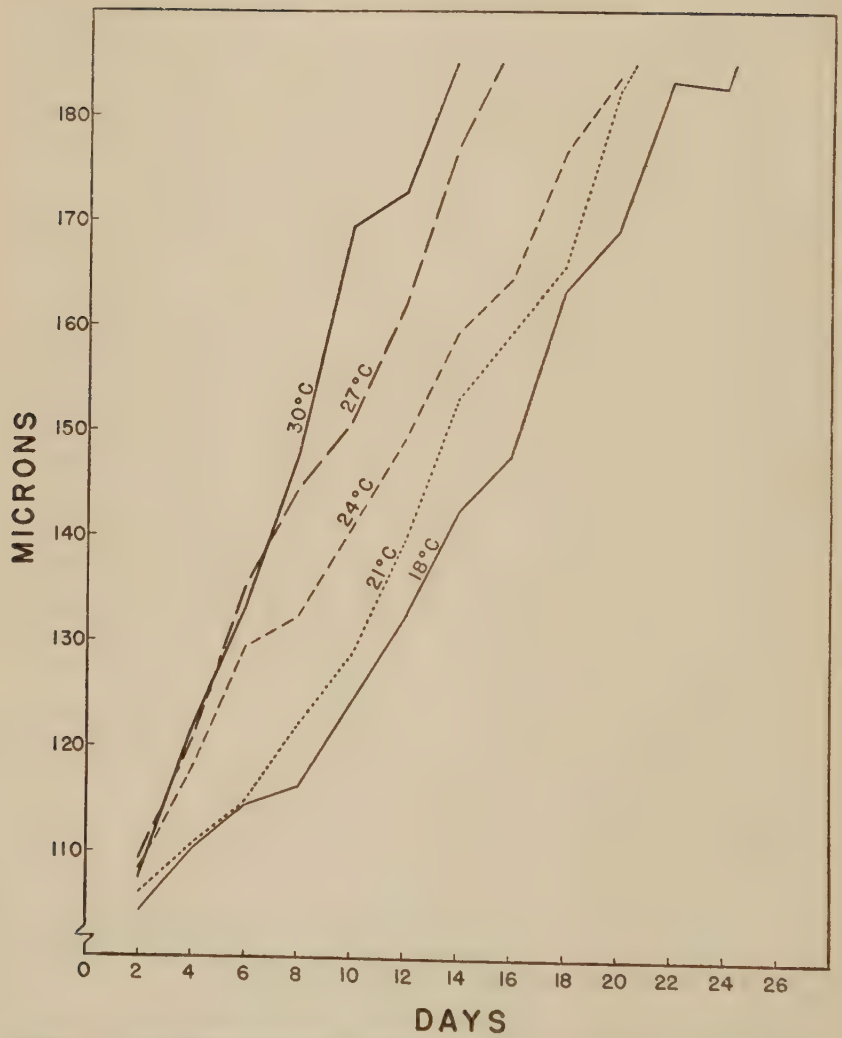

Figure 2. Mean length of larvae of different ages grown at five constant temperatures. Experiment 2.

The length at which metamorphosis took place in our cultures ranged from approximately 175 to 236 μ, occurring most commonly between 200 and 210 μ. The largest larvae did not always metamorphose first. In several cultures some comparatively small individuals of only approximately 180 μ did metamorphose, while larger

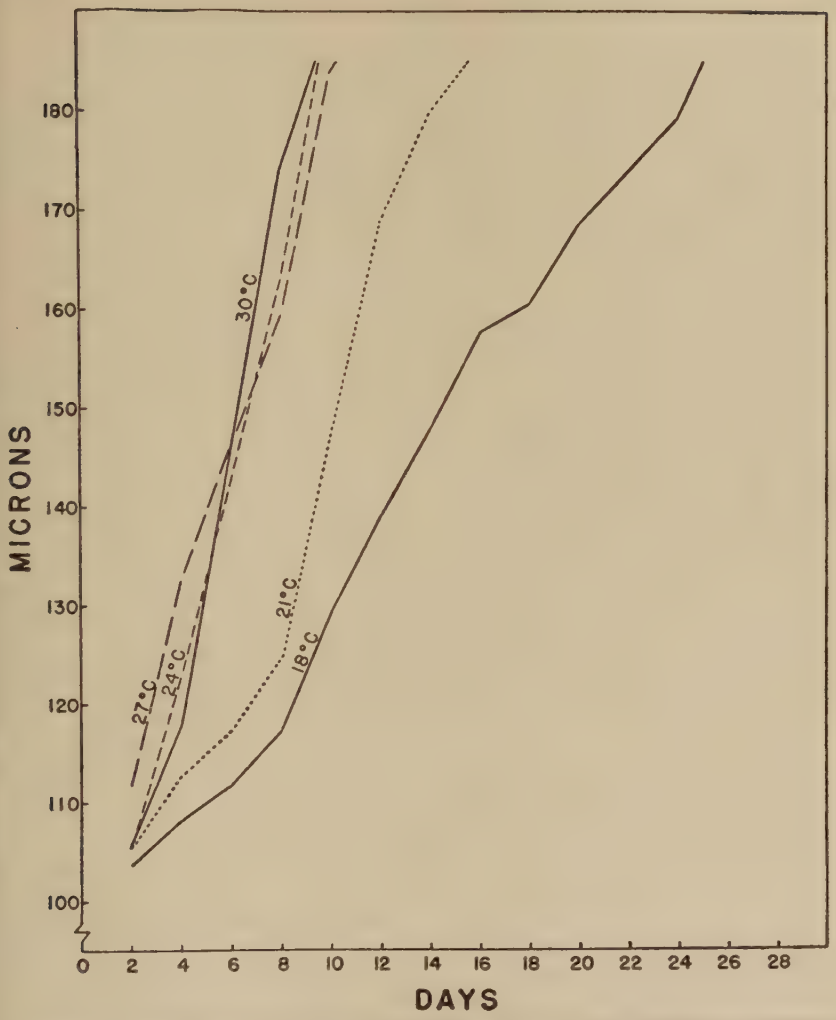

Figure 3. Mean length of larvae of different ages grown at five constant temperatures. **Experiment 3.**

larvae of more than 200 μ still continued swimming, at the same time displaying a powerful velum and a comparatively small foot.

In the course of these experiments we tried to determine whether larvae grown at low temperatures, such as 18.0° C, would reach a larger size before setting than larvae grown at higher temperatures. Some of the preliminary experiments did indicate a tendency of this

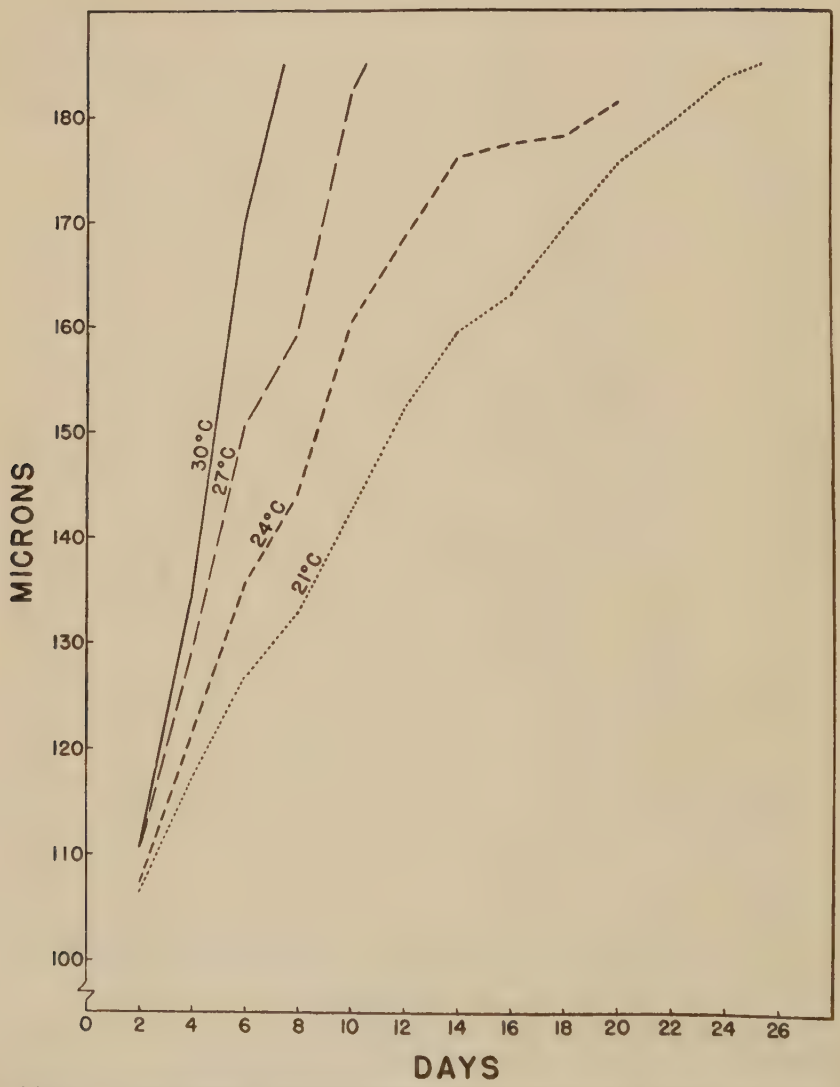

Figure 4. Mean length of larvae of different ages grown at four constant temperatures. Experiment 4.

type, but further and more extensive experiments did not support this contention.

With exception of the 30.0° C group, the results of the first experiment showed that the rates of growth of the other four temperature

groups closely resemble each other, indicating that, within the temperature range of 18.0 to 27.0° C, differences in temperature do not always significantly affect the rate of growth (Fig. 1). When plotted, the data do not resemble the exponential growth curves offered by Medcof (1939) for the growth of larvae of *O. virginica.* Moreover, contrary to the findings on some other lamellibranchs (Seno, et al., 1926), the larvae kept at 30.0° C did not die but showed healthy and rapid growth, some of them reaching the setting stage during the seventh day after fertilization, i. e., considerably ahead of the cultures kept at lower temperatures.

Subsequent studies (Figs. 2, 3 and 4) showed that the results of Experiment 1 were somewhat atypical. Nevertheless, they are included here not only for comparison and discussion but partly to demonstrate the possible deviations that may occur in this type of study. Naturally, we sought for an explanation of the peculiar results observed in Experiment 1. Critical analysis of the methods and procedures used during the experiment showed that the only factors that varied from culture to culture were temperature, and possibly aeration. Other factors, such as number of larvae, quantity of food, salinity, pH, amount of light, etc., were identical in all cultures. Of course, the differences in the temperatures were the basic part of the experiment. The differences in aeration, the only factor that was not rigidly controlled, had to be properly evaluated. The following experiment was designed to evaluate the importance of such differences.

Several cultures of larvae were started under identical conditions except for the degree of aeration. Some crocks were aerated very vigorously, the water surface resembling that of boiling water in a bucket; other crocks were aerated only feebly; the third received no aeration whatsoever with exception of unavoidable splashes that occurred during a water change every second day. It was found that vigorous aeration of the cultures was unnecessary after the larvae had reached the straight hinge stage. Actually, clean and carefully attended cultures were brought to the setting stage without continuous aeration. The larvae of the unaerated cultures showed approximately the same percentage of survival, grew at the same rate and began setting at the same time as the feebly or strongly aerated cultures which, in turn, showed no significant differences. Obviously, since the differences in degree of aeration in the cultures of Experiment 1 were incomparably smaller than those of the cultures of the specially designed experiment, we may conclude that aeration was not responsible for differences in the rates of growth of larvae in the different cultures of Experiment 1.

Experiments 2, 3 and 4 showed agreement in general, the rate of growth of the larvae being more rapid at high than at low temperatures (Figs. 2, 3 and 4). However, even in these experiments certain discrepancies were noted. For example, in Experiment 2, on the sixth day, the mean length of the larvae grown at 27.0° C was somewhat greater than that of the 30.0° C group (Fig. 2). In Experiment 3, until the sixth day, the mean rate of growth of the larvae was also

TABLE I. Number of Days Needed after Fertilization for the Beginning and for the Completion of Setting of Larvae at Different Temperatures in Each of Four Experiments; Range in Days between the Beginning and Completion of Setting, and the Maximum Number of Days during Which Setting May Extend in Cultures Grown at the Same Temperatures

Temp. °C	*Days*				*Range in days*	*Number of days*
	Expt. 1	*Expt. 2*	*Expt. 3*	*Expt. 4*		
18.0	16–28	24–30	19–30	—	16–30	14
21.0	14–24	20–26	17–22	18–28	14–28	14
24.0	14–22	17–22	11–14	14–22	11–22	11
27.0	14–20	13–18	9–14	10–14	9–20	11
30.0	7–12	9–16	7–14	7–12	7–16	9

more rapid at 27.0° C than that at 30.0° C (Fig. 3). Furthermore, even the 24.0° C group of this experiment was, for some time, growing more rapidly than the 30.0° C group.

To summarize the results of all four experiments, the arithmetic means of all the length measurements for each temperature at definite times were taken and the curves fitted by the method of moving averages (Fig. 5). The curves showed that growth of the larvae was more rapid at high than at low temperatures. However, the upper portions of the curve did not suggest that the distances between the terminal points of the curves significantly increased as the temperature decreased, as was shown by Medcof (1939) for oyster larvae.

At 30.0° C, setting of larvae in three experiments began as early as the seventh day after fertilization, but in one it was delayed until the ninth (Table I). The entire population of the cultures kept at this temperature metamorphosed within five to seven days after the beginning of setting (Table II). However, the range in days between the beginning and completion of setting at this temperature, as based on all four experiments, extended from the seventh to the 16th day after fertilization and covered a period of nine days (Table I).

At 18.0° C, the earliest beginning of setting was recorded 16 days after fertilization, the latest beginning 24 days after fertilization (Table I). The range in days between the beginning and completion of setting at this temperature extended from the 16th to the 30th day after fertilization, thus covering a period of 14 days. While in Experi-

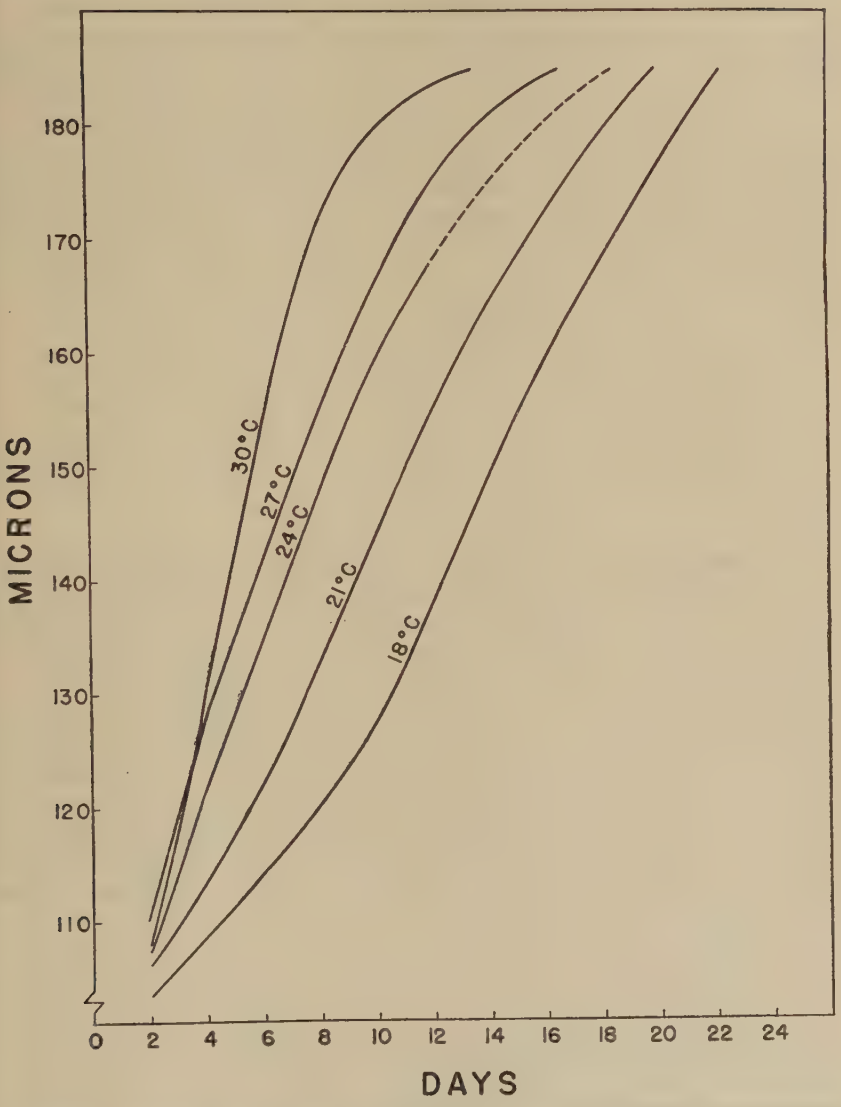

Figure 5. General trend of increase in length of larvae grown at different temperatures, as based on measurements made in four experiments.

ments 1 and 3 setting at 18.0° C continued for 12 and 11 days respectively, in Experiment 2 it was completed in only six days, thus indicating considerable variation in the behavior of a population of clam larvae, presumably kept under identical conditions.

The number of days needed after fertilization for the beginning and completion of setting of larvae at the three intermittent temperatures of 21.0, 24.0 and 28.0° C are also given in Table I. With exception of Experiment 1, where setting at three different temperatures began on the same (14th) day, in general the number of days increased with a decrease in temperature. Furthermore, even in Experiment 1, the range of setting in days increased with a decrease in temperature. Thus, for example, while setting was completed in 20 days after fertilization at 27.0° C, at 21.0° C it continued until the 24th day (Table I).

TABLE II. Number of Days Elapsing between the Beginning and the End of Setting in the Cultures Kept at Different Temperatures

Temp. °C	*Number of days*			
	Expt. 1	*Expt. 2*	*Expt. 3*	*Expt. 4*
18.0	12	6	11	—
21.0	10	6	5	10
24.0	8	5	3	8
27.0	6	5	5	4
30.0	5	7	7	5

The number of days elapsing between the beginning and the end of setting in cultures kept at different temperatures did not always follow a definite pattern. Experiment 1 was the only one in which there was a definite trend showing that the number of days needed for the completion of setting of the entire larval population decreased with an increase in temperature (Table II). In that experiment, 12 days were needed to complete the setting at 18.0° C, while at 30.0° C setting of the entire population was completed in five days. In Experiment 2, however, no such relation was found. In fact, setting was completed within a somewhat shorter period at 18.0° C than at 30.0° C. Experiments 3 and 4 also present in this respect a somewhat inconsistent picture, although Experiment 4 generally resembles the trend found in Experiment 1 (Table II).

Our studies showed that the larvae, which came from the same spawnings and which were kept in the same crocks, obviously under identical conditions, showed great variations in size. Taking as an example the data of Experiment 2, one will find that, early in the experiment, on the second day after fertilization, the range in length of larvae was comparatively small (Table III). At a temperature of 18.0° C it ranged between 93 and 107 μ, while at 30.0° C it extended from 93 to 121 μ. However, as the experiment progressed, the difference between the minimum and maximum sizes increased. Toward the end of the experiment the length range of the larvae in the 18.0° C culture extended from 150 to 221 μ and in the 30.0° C culture from 150

to 207 μ. At some intermediate temperatures, for example that of 21.0° C, the differences in the length of the larvae during the last days of the experiment were even greater, extending from 136 to 236 μ (Table III).

The differences in sizes of larvae of the same age, presumably grown under identical conditions, become even more striking if the data from all four experiments are analyzed. Considering, for the sake of convenience, the measurements of the larvae of only two temperature groups, namely 21.0 and 30.0° C, we will again see that the larvae differed in length by only a few microns at the early stage of cultiva-

TABLE III. Minimum and Maximum Lengths of Larvae of *V. mercenaria* Recorded Every Second Day in Cultures of Experiment 2. Data for Each Date and Temperature Are Based on 100 Measurements

Days	*Temperature*									
	18.0° C		*21.0° C*		*24.0° C*		*27.0° C*		*30.0° C*	
	Min.	*Max.*	*Min.*	*Max.*	*Min.*	*Max.*	*Min.*	*Max.*	*Min.*	*Max.*
2	93	107	93	114	86	114	100	121	93	121
4	100	121	100	121	100	136	100	136	100	143
6	100	143	100	129	114	150	107	164	93	164
8	100	129	107	136	121	164	114	172	107	193
10	107	143	107	157	114	164	107	186	129	207
12	107	150	114	164	114	172	114	207	121	214
14	107	164	114	179	121	186	136	214	150	207
16	114	179	121	186	121	193	129	207	—	—
18	107	200	107	193	150	193	136	214	—	—
20	121	200	136	214	129	214	—	—	—	—
22	143	207	136	221	—	—	—	—	—	—
24	129	207	136	228	—	—	—	—	—	—
26	150	221	136	236	—	—	—	—	—	—
28	150	221	—	—	—	—	—	—	—	—

tion, on the second day, whereas several days later these differences covered practically the entire larval size-range extending from small straight hinge larvae of approximately 100 μ to full grown larvae in excess of 200 μ. For example, on the eighth day the sizes of the larvae grown at 30.0° C ranged from 107 to 226 μ (Fig. 6). Similarly, for the culture kept at 21.0° C the length of the larvae measured on the 18th day ranged from 107 to 221 μ.

Sometimes, as is shown for the temperature of 30.0° C (Fig. 6), the range of the larval sizes sharply contracted during the last days of the experiments. This happened partly because the larger individuals were rapidly setting and disappearing from the free-swimming population and partly because the undeveloped slow-growing larvae, usually defective in some respects, were dying off just as rapidly.

The data offered in Fig. 6 give only the extremes of the larval sizes without showing the prevalence of certain size-groups in the larval population. An example of such length-frequency distributions of

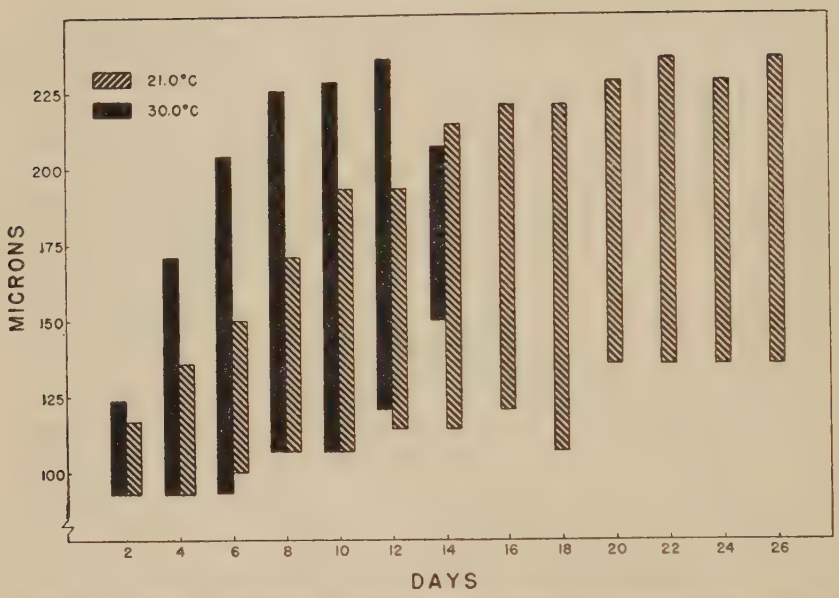

Figure 6. Extent of variations in length of larvae on different days of cultivation. Based on measurements of larvae grown at 21.0 or 30.0° C in all four experiments.

larvae is given in Fig. 7, which is based upon the measurements of the larvae grown at 18.0, 24.0 and 30.0° C in Experiment 2. The temperature selected represented the lowest, the highest, and the average of the five temperature classes. Experiment 2 was chosen as the example because it approaches most closely the mean of all four experiments. At the end of two days the length-frequency distribution of the larvae of the three cultures was relatively uniform, occupying a comparatively narrow range and showing a modal class of approximately 107 μ. Between the fourth and sixth days, however, the differences between the length-frequency distribution of the larval population of the three cultures had already become prominent. The difference was especially evident in the case of the modal classes. While for the 18.0° C group this class was 114 μ, for the 24.0 and 30.0° C groups these classes were 129 and 143 μ respectively (Fig. 7).

As the experiment progressed, the differences in length-frequency distribution of the larvae from the three cultures remained significant. In all instances the lengths of the modal classes of cultures grown at higher temperatures were greater than those at lower ones.

On the 18th day the comparison could be continued only between the 18.0 and 24.0° C cultures because the larvae in the culture of 30.0°

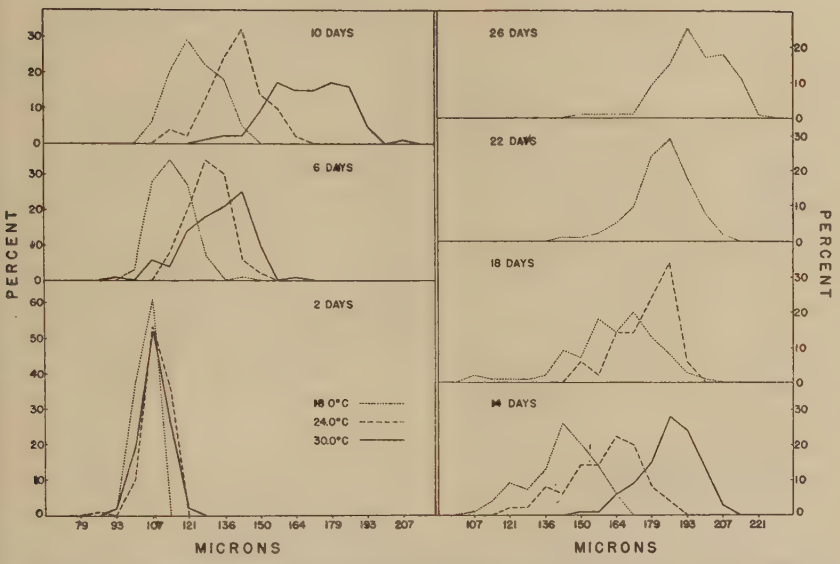

Figure 7. Length-frequency distribution (expressed in per cent) of larvae of different ages grown at temperatures of 18.0, 24.0 or 30.0° C. Experiment 2.

C had already set. For a similar reason the length-frequency distribution of the larvae after the 22nd day was available only for the 18.0° C culture.

The length-frequency distributions of larvae grown at the same temperatures but in four different experiments did not always closely resemble each other. For example, examining the length measurements of larvae grown at a temperature of 24.0° C in each of the four experiments, we found that the differences in the modal classes of the four cultures became apparent as early as the fourth day (Fig. 8). At eight days these differences became even more sharply defined. On the 12th day, while the cultures of Experiments 1 and 4 showed considerable agreement, and while the culture of Experiment 2 was not greatly different from those two, the culture of Experiment 3 definitely deviated from the others. The difference was not only in the size-range of larvae but also in the size of the modal class which measured 207 μ, as compared with 164 μ of the modal classes in the cultures of Experiments 1 and 4.

The culture of Experiment 3 set on the 14th day; therefore the comparisons made on 16 and 20 days are based only on the cultures of Experiments 1, 2 and 4 (Fig. 8). At 16 days the cultures of Experiments 1 and 4 showed close agreement, while the culture of Experiment

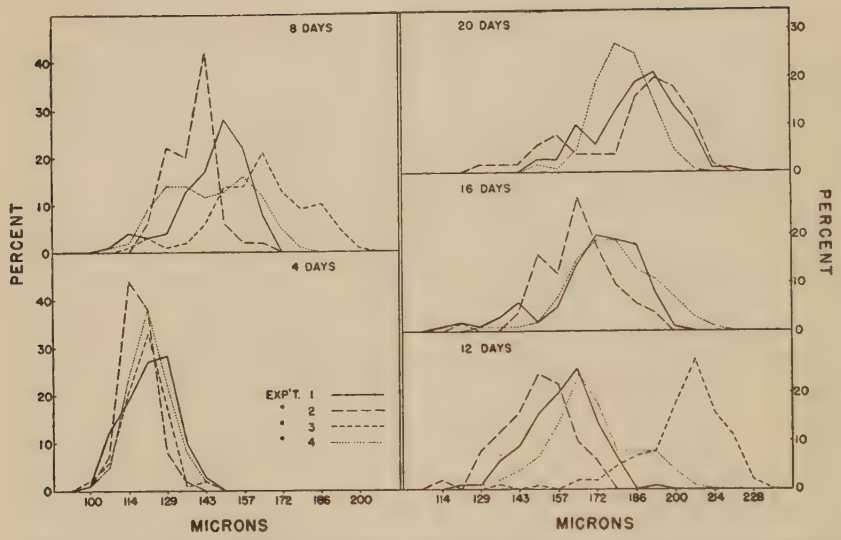

Figure 8. Length-frequency distribution (expressed in per cent) of larvae of different ages grown at a temperature of 24.0° C in the four experiments.

2 differed somewhat from the other two. However, at 20 days the agreement which existed previously between the cultures of Experiments 1 and 4 disappeared because, while the modal class of the culture of Experiment 1 showed a considerable increase, that of the culture of Experiment 4 remained practically the same. Meanwhile, the culture of Experiment 2 displayed rapid growth, thus catching up with the culture of Experiment 1.

On the basis of this comparison it may be concluded that the length-frequency distribution of the larvae grown at the same temperature in the four experiments, and otherwise kept under identical conditions, nevertheless showed considerable differences. The question naturally arises as to whether, regardless of all the precautions taken, there might have been some not-easily-identifiable differences that existed during the conduct of the four experiments which caused the lack of uniformity in the results. As far as the methods and procedures were concerned, it is certain that they were the same in all experiments. The same holds true in regard to salinity, pH, and other presumably important qualities of the water used. However, since the experiments were conducted one after another during several months rather than simultaneously, it is possible that the water used in the different experiments did differ in some respects. Even if the water were always filtered through a thick layer of cotton, thus removing most of the

plankton, nevertheless minute quantities of micro-plankton could pass through the filter. It is considered possible that the differences in quantity and quality of this micro-plankton may have accounted for the differences noted in the four experiments.

This suggestion may not appear to be well founded when it is remembered that the quantity of micro-plankton that could pass through the filters would be so small that it could not add appreciably to the food supply of our dense cultures of larvae. Nevertheless, it should not be disregarded, for the material passing through the filter might have been carrying traces of some substances necessary for the normal development of the larvae. Also, it is considered possible that at different times the water itself contained certain dissolved substances which, in a manner not yet understood, affected the rate of development of bivalve larvae. These possibilities merit careful study.

We shall now refer to the results obtained in experiments in which the eggs or larvae were kept at 15.0 or 33.0° C. If recently discharged eggs were placed in water of 15.0° C within three hours after fertilization, virtually none of them would undergo normal development which would result in the formation of straight hinge larvae. Some, however, would develop into trochophore larvae, usually of abnormal appearance.

If the eggs were kept at a room temperature of about 20.0–21.0° C for three to four hours after fertilization and then placed in water of 15.0° C, a few would develop into straight hinge larvae. However, the majority of these larvae would be abnormal and would soon die.

Fertilized eggs kept at room temperature for six or nine hours before being subjected to a temperature of 15.0° C gave a greater number of individuals reaching the straight hinge larval stage, but nevertheless, the majority developing that far would be abnormal and would soon perish. However, if the eggs and the resulting larvae were kept at room temperature for two days until the straight hinge stage was well formed, after which the larvae were then placed in water of 15.0° C, many of these larvae would survive. Regardless of slow growth, it is possible that, under certain conditions, some of these larvae would reach the stage of metamorphosis.

The experiments demonstrated rather conclusively that the zygotes of *V. mercenaria* in early stages of cleavage, for normal development and survival, require a somewhat higher temperature than the zygotes or larvae in later stages.

Our results of culturing eggs and larvae of *V. mercenaria* at a relatively low temperature are in close agreement with those of Seno, et al. (1926); they found that only a few of the eggs of *Ostrea gigas* kept at

about 16.0° C developed into shelled larvae, most of which would be abnormal and would soon die. At about 14.0° C, however, the segmentation of the eggs was so abnormal that none developed into straight hinge larvae.

At the other end of our temperature range, 33.0° C, an abnormal development and heavy mortality occurred if fertilized eggs were immediately transferred to water of such a high temperature. However, if the eggs and larvae that hatched were allowed to develop at room temperature for 48 hours and were then transferred to water of 33.0° C, a rapid normal development of larvae followed similar to that noticed in the cultures kept at 30.0° C. In general, these observations, as well as those made at 15.0° C, fully coincide with the view expressed many years ago by Pelseneer (1901) that young cleavage stages of molluscan eggs require a narrower temperature range than the later stages.

In the course of our experiments, many thousands of measurements were made of the length and width of the veliger larvae of different ages and sizes. Part of these data, consisting of measurements of 1,250 larvae grown at a temperature of 21.0° C in Experiments 1, 2 and 3, were used for determining the length-width relationship from early straight hinge stage to metamorphosis. This relationship is shown by the curve given in Fig. 9. The numerals through which the curve is drawn indicate the frequency of occurrence of larvae of certain lengths and widths. The character of the curve closely approaches a straight line. The data used in the construction of the curve fall into distinct modal groups with very little degree of dispersion. As already pointed out, some of the dispersion may be due to the position of the larvae on the slide during the measurement.

The size of the smallest straight hinge larvae incorporated in the curve was 86 x 64 μ, the largest 236 x 228 μ (Fig. 9). We may mention that, in addition to the 1,250 measurements used for the construction of this curve, we have the measurements of over 20,000 other larvae grown in these experiments and in many other experiments conducted since 1948. Regardless of the extremely varied ecological conditions under which these experiments were conducted, we have never found a larva more than 240 μ in length. This makes it highly improbable that the larvae of *V. mercenaria* may grow up to 448.5 μ long before metamorphosis, as reported by Stafford (1912). Furthermore, the shapes and dimensions of larvae of different sizes given by Stafford as those of *V. mercenaria*, when compared with those of larvae grown in our laboratory from the eggs of adult clams made to spawn under controlled conditions, show beyond all doubt that Stafford mistook the larvae of some other bivalves for those of *V. mercenaria*.

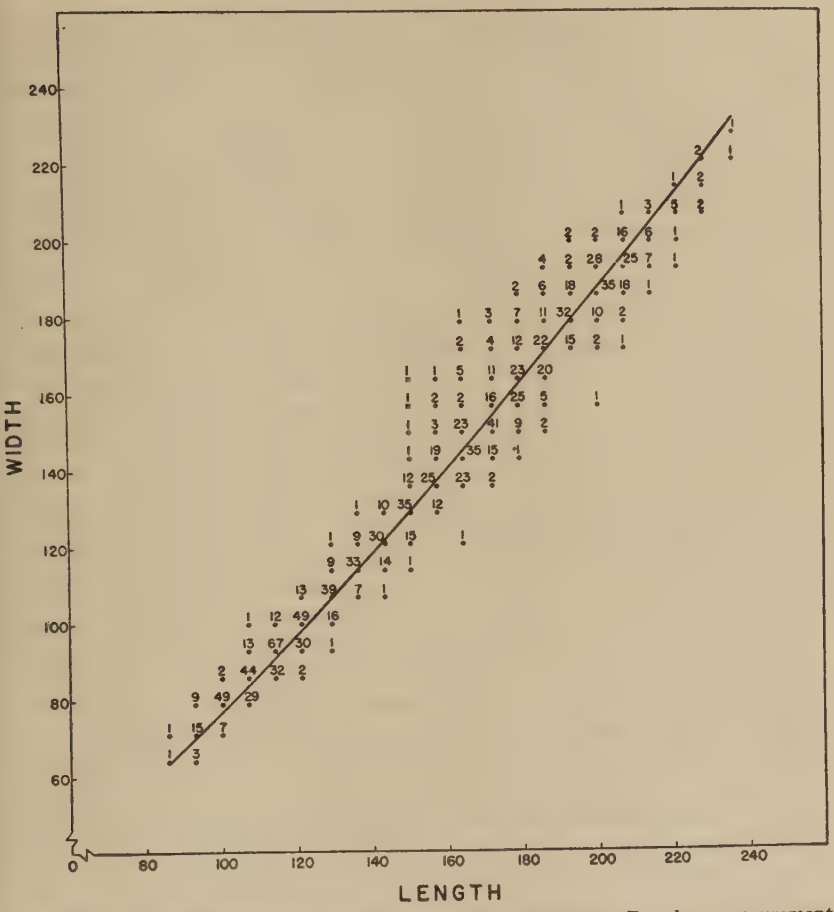

Figure 9. Length-width relationship of larvae of different sizes. Based on measurements of 1,250 larvae. Measurements in microns.

Similar remarks may be made about the conclusions of Sullivan (1948) on the size and shape of larvae of *V. mercenaria*. However, in a recent letter, Miss Sullivan clarifies the issue by writing as follows:

> It seems likely then that I have confused the larvae of *P. morrhuana* and *V. mercenaria*. This mistake is attributable to the fact that the newly settled spat of both types were very scarce in my collections. It was, furthermore, difficult to distinguish between the two types of very young spat or to identify either type with certainty.
>
> If it is the case then that my larva, *P. morrhuana*, is really *V. mercenaria*, it follows that the settling size of *Venus* larvae in Malpeque Bay corresponds reasonably well with that of *Venus* larvae in your cultures.

Incidentally our disagreement with Sullivan on the general characteristics of the larvae of *V. mercenaria* extends also to their color. Sullivan (1948) considers the color as a distinctive feature which she uses for identification of larvae of lamellibranchs. Actually, as already mentioned, we found that the color of larvae in any stage of development could be easily changed by feeding the larvae different types of food. Therefore, in nature, where the predominating species of micro-plankton may change daily, correspondingly frequent changes in the color of larvae may be expected.

In concluding, we would like to incorporate some observations which we think are of importance in studies of the growth and development of *V. mercenaria* and probably of other lamellibranch larvae as well. The first of these deals with the relative merits of detritus as food of larvae. As is generally known, during the last few years some evidence has been gathered to show that detritus was the principal food of lamellibranchs (Coe, 1948). To determine the relative importance of detritus as food of larvae of *V. mercenaria*, experiments were designed in which some cultures of larvae were fed *Chlorella*, others a mixture of *Chlorella* and sulfur bacteria, and still others were given a large quantity of detritus of one of the two types. Type 1 consisted of detritus collected from the bottom of the large tank in which plankton was grown for eight months previous to collection of the sample. During that long period, many generations of plankton died and fell on the bottom, thus creating a heavy layer of detritus which measured in excess of one-quarter of an inch. This material was filtered to remove large particles which could not be utilized and was then fed to the larval cultures. The second type of detritus was collected during the low tidal stages from the bottom of the tidal pools formed on the tidal flats of Milford Harbor. This detritus was also filtered to remove the large particles and was then fed to the larvae.

The experiments showed that there was no evidence whatsoever to support the contention that the larvae of *V. mercenaria* would grow better on detritus than on living *Chlorella* or on a mixture of living *Chlorella* and sulfur bacteria. As a rule, the cultures grown on detritus were always much inferior to those fed with *Chlorella* or its mixtures with bacteria, and the larvae usually died from starvation before they reached the stage of metamorphosis.

The second observation concerns the density of the larval population in the cultures. As already mentioned, our experiments usually began with approximately 50 eggs per cc of water. This was a much heavier concentration than that practiced or advocated by other investigators who have usually emphasized the danger of overcrowd-

ing. Our concentrations, therefore, may appear to those workers to be unrealistically dense. However, since cultures of these densities are carried at our laboratory to the stage of metamorphosis as a matter of routine, and since on many occasions we grew successfully even denser cultures, we think that in some instances the danger of overcrowding larvae of some species of lamellibranchs may not be as acute as believed. Apparently, in properly kept cultures a great majority of the larvae can survive such overcrowding, display a normal rate of growth, and reach the setting stage in the same time as larvae of much less populated cultures.

SUMMARY

1. Larvae of *V. mercenaria* were grown to metamorphosis in four experiments at the constant temperature of 30.0, 27.0, 24.0, 21.0, 18.0° C ± 1.0° C. Observations on development of eggs and growth of larvae were also performed at 33.0 and 15.0° C ± 1.0° C.

2. The size of the smallest straight hinge larvae found was 86 x 64 μ, the largest 236 x 228 μ.

3. Within the temperature range of 18.0 to 30.0° C ± 1.0° C, the rate of growth of larvae was generally, but not always, more rapid at high than at low temperatures. Small differences in temperature, such as one or two degrees, or sometimes even more, were not as important in affecting the rate of growth as was previously thought.

4. At 30.0° C, setting of larvae began in some experiments as early as the seventh day after fertilization. Setting of the entire larval population kept at this temperature was accomplished within five to seven days after its beginning.

5. At 18.0° C, the earliest beginning of setting was recorded 16 days after fertilization, the latest 24 days after fertilization. At other intermittent temperatures setting of larvae was within the bounds indicated by the two extremes.

6. The length at which metamorphosis took place ranged from approximately 175 to 236 μ, occurring most commonly between 200 and 210 μ. There was no indication that the larvae grown at lower temperatures were reaching larger size before setting than those grown at higher temperatures.

7. Larvae which came from the same source and which were kept under identical conditions showed great variation in size. In some instances the length of the larvae in an old culture ranged from about 100 μ to that of full grown larvae measuring in excess of 200 μ.

8. The length-frequency distribution of larvae grown at the same temperature but in four different experiments showed considerable variation. These variations were found in the range of larval lengths and also in the lengths of the modal classes.

9. If, immediately after fertilization, the eggs of clams were placed in water of a temperature of 15.0° C ± 1.0° C, virtually none of them would undergo normal development leading to the straight hinge stage. However, if the eggs were kept at room temperature for nine hours before they were subjected to the above temperature, some of them would develop into straight hinge larvae.

10. Eggs placed in water of 33.0° C ± 1.0° C soon after fertilization would show abnormal development and heavy mortality. However, if the zygotes were kept at room temperature of about 22.0° C for about two days after fertilization and were then transferred to the higher temperature, a rapid normal development of larvae would follow.

11. Young cleavage stages of clam eggs occur within a narrower temperature range than the later stages.

12. The color should not be considered as a distinctive feature to be used in the identification of lamellibranch larvae, because it changes easily depending on the color of the organisms eaten by the larvae.

13. No evidence was found to support the contention that organic detritus is a better food for larvae than living phytoplankton. Two types of detritus, one composed mostly of dying and decomposing plankton grown under laboratory conditions, the other collected from the bottom of tidal pools, were fed to the larvae, but such feeding caused their slow starvation and death.

14. The degree of aeration was found to be unimportant in affecting the rate of survival and rate of growth of clam larvae. Clean and carefully attended cultures could be brought to the setting stage without continuous aeration.

15. Overcrowding of larval cultures of *V. mercenaria* is not too easily achieved. As a rule, our cultures contained 50 larvae per cc of water, and several cultures, in which the concentration of larvae was more than 100 per cc of water, were grown to metamorphosis.

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ETIOLOGICAL STUDIES ON OYSTER MORTALITY

I. *Nematopsis ostrearum* Prytherch 1940 (Sporozoa : Porosporidae)[1]

By

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ABSTRACT

Oysters from the major producing area of Louisiana were found to be 100% infected with the gregarine parasite *Nematopsis ostrearum;* those from a check station in Pencacola Bay, Florida, were found to be 95.1% infected. In Louisiana, the population of *N. ostrearum* was found to be higher in the area east of the Mississippi River. *N. ostrearum* infections in oysters increased significantly during summer months in areas of relatively low oyster mortality. It was concluded on indirect and negative evidence that *N. ostrearum* was not a controlling factor responsible for the condition of oysters or for their extensive mortalities in Louisiana waters.

INTRODUCTION

During extensive investigations on causes of oyster mortalities in Louisiana coastal waters, the authors studied the intensity and distribution of *Nematopsis ostrearum* Prytherch in its secondary host, the oyster. This phase of our etiological study is concerned only with the parasite *N. ostrearum.*

Both Prytherch (1938) and Kudo (1946) have described the life cycle of the oyster parasite which Prytherch later (1940) described as a new species, *N. ostrearum*, and which we consider to be the species observed in this study. Sprague (1949), recognizing two species, described *N. prytherchi*, which occurs simultaneously with *N. ostrearum* in the secondary host but which is concentrated in the gills. With this latter species we are not concerned in this study.

Systematic studies were made on oysters from selected locations in Louisiana and Florida. The incidence and degree of infection were determined and the results were compared with mortality and with the Index of Condition determinations.

[1] Contribution Number 5 from the Contractual Research Program, Division of Oysters and Water Bottoms, Louisiana Department of Wild Life and Fisheries.

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MATERIALS AND METHODS

Twenty-one stations were established in Louisiana (Fig. 1) and one at Pensacola, Florida.[3] The stations were sampled at regular intervals in 1947 and 1948 and sporadic checks were made in 1949. Because of the extent of the territory, an amphibious plane was used to transport a standard sample of 25 oysters from the collection point to the laboratory for immediate analysis and examination.

Figure 1. Outline Map showing the location of stations and the five major drainage areas in the eastern oyster-producing region of Louisiana.

The technique employed for the microscopic examination of the tissue was as follows. A square centimeter of mantle tissue, ventrally adjacent to the adductor muscle, was dissected from each of ten oysters, and each sample tissue was then individually mounted in a 20% NaOH solution between two firmly compressed microscope slides. After each tissue was partially digested (10 minutes), it was studied under the low power of a compound microscope equipped with a Whipple Ocular Micrometer. By use of the mechanical stage, ten microscope fields

[3] Laboratory of the U. S. Fish and Wildlife Service, where space was made available to the State of Louisiana for the purpose of conducting independent investigations.

were examined and the number of cysts included in the micrometer field were counted and recorded. At least ten oysters were thus examined, one sample having been taken from each. The results were averaged to give the intensity of infection.

The following arbitrary values were selected on the basis of accumulated experience in order to facilitate an understanding of the comparative degree of infection that was found to be present in Louisiana and Florida oysters:

0–19 cysts per W-M field	very light
20–39 cysts per W-M field	light
40–59 cysts per W-M field	medium
60–79 cysts per W-M field	heavy
80–99 or more per W-M field	very heavy.

The same oysters were used for measuring the Condition Index (Hopkins, 1938). The Mortality Index for the respective stations in Louisiana was determined over a period of 30 months by sampling with a standardized procedure, expressed in per cent. This procedure consisted of tonging or dredging oysters at random at a given station until a one-half standard oyster bushel measure was obtained. Mortality was determined by counting the recently dead oysters. Normally the valves of the oyster are held together by an elastic hinge ligament, but at death the two valves stand or "gape" open, the oyster meats disappear quickly, so that all that remains is two hinged valves, which are called "boxes." The live oysters were separated from the "boxes." The mortality results at the Pensacola station were determined from the control tanks of other oyster experiments. A total of 1600 oysters was used.

RESULTS

The microscopic examination of 723 live oysters from 30 locations in Louisiana coastal waters showed a 100% infection; no dead oysters were examined. In Florida, 260 live oysters were examined, 95.1% being infected; of 495 dead oysters examined, 94.2% had been infected.

The results of the Louisiana examinations, the Condition Index determinations, and the mortality percentages are summarized in Table I. The results of the Florida investigations are summarized in Table II. For clarity in discussion, the results in Table I are arranged and summarized according to the natural drainage areas of the oyster-growing regions (Fig. 1, Table III). Table IV contains the results from the studies of all Louisiana stations.

Our data show no correlation of *N. ostrearum* infection with salinity, dissolved oxygen, and hydrogen-ion concentration of the water. These factors were carefully checked from the tank experiments conducted at the Pensacola Laboratory.

TABLE I.—Infection of Louisiana Oysters with *Nematopsis ostrearum*, Compared with the Indices of Condition and Mortality

Station Number	*Location*	*Date of Sampling (month-year)*	*Av. No. Cysts per Sample*	*Condition Index per Sample*	*Mortality Index per Station (Total)*	*Comparative Intensity of Infection*
1	Cabbage Reef	10–47	61.1	—		Heavy
		3–48	41.2	8.6	5.5	Medium
		7–48	125.5	6.4		Very Heavy
		12–48	57.9	5.7		Medium
2	Bayou Pierre	10–47	51.2	—		Medium
		3–48	42.0	8.1	30.5	Medium
		7–48	122.4	7.0		Very Heavy
		12–48	66.7	4.7		Heavy
3	Grand Pass	10–47	75.1	—		Heavy
		3–48	48.6	9.6	9.5	Medium
		7–48	98.7	6.3		Very Heavy
		12–48	31.9	4.8		Light
4	Black Bay	3–48	75.2	3.8	5.8	Heavy
		7–48	69.7	7.8		Heavy
		12–48	32.6	4.9		Light
6	American Bay	10–47	41.2	—	6.6	Medium
		3–48	64.5	5.5		Heavy
		7–48	63.6	8.2		Heavy
		12–48	116.1	3.3		Very Heavy
7	California Bay	10–47	40.6	—	11.5	Medium
		3–48	31.0	4.4		Light
		7–48	123.8	8.3		Very Heavy
		12–48	83.7	3.9		Very Heavy
8	Quarantine Bay	10–47	31.0	—	25.2	Light
		3–48	36.8	5.7		Light
		7–48	79.6	6.9		Heavy
		12–48	33.3	3.9		Light
9	Grand Bay	10–47	17.2	—	43.5	Very Light
		3–48	15.7	9.5		Very Light
		7–48	165.1	8.4		Very Heavy
		12–48	30.1	6.3		Light
10	Sandy Point	10–47	42.1	—	21.8	Medium
		3–48	52.0	10.1		Medium
		7–48	41.0	3.3		Medium
		12–48	32.2	7.4		Light
11	Skipjack Bay	10–47	18.0	—	39.0	Very Light
		3–48	—	12.2		
		7–48	21.1	4.1		Light
		12–48	21.3	7.7		Light

TABLE I—*Continued.*

Station Number	*Location*	*Date of Sampling (month-year)*	*Av. No. Cysts per Sample*	*Condition Index per Sample*	*Mortality Index per Station (Total)*	*Comparative Intensity of Infection*
13	Bayou Scofield	10–47	21.1	—		Light
		3–48	24.2	12.2	42.0	Light
		7–48	42.5	5.8		Medium
		12–48	45.1	8.9		Medium
16	Bastian Bay	10–47	30.5	—	80.1	Light
		3–48	29.6	12.8		Light
		7–48	24.1	6.0		Light
		12–48	28.7	10.6		Light
18	Rattlesnake Bayou	10–47	20.7	—	32.8	Light
		3–48	—	—		
		7–48	31.2	6.4		Light
		12–48	22.7	6.5		Light
20	St. Mary's Point	10–47	—	—		
		3–48	31.8	7.2	23.3	Light
		7–48	36.2	4.0		Light
		12–48	54.9	4.3		Medium
21	Bassa-Bassa Bay	10–47	—	—		
		3–48	17.9	8.8	36.0	Very Light
		7–48	25.3	6.2		Light
		12–48	17.8	9.0		Very Light
22	Lower Barataria	10–47	26.7	—	58.1	Light
		3–48	33.4	9.6		Light
		7–48	52.6	9.2		Medium
		12–48	88.6	7.1		Very Heavy
23	Lake Felicity	10–47	—	—		
		3–48	43.2	9.1	22.6	Medium
		7–48	58.0	4.7		Medium
		12–48	15.0	5.8		Very Light
23A	Lake Pelto	10–47	32.5	—		Light
		3–48	34.1	7.4	—	Light
		7–48	44.8	4.9		Medium
		12–48	15.4	6.4		Very Light
24	Sister Lake	10–47	18.2	—	8.4	Very Light
		3–48	13.3	5.5		Very Light
		7–48	71.3	5.0		Heavy
		12.48	10.4	5.3		Very Light
25	Four League Bay	10.47	—	—		
		3–48	22.5	7.4		Light
		7–48	33.5	4.8	—	Light
		12–48	21.6	5.5		Light
25A	Oyster Bayou	10–47	—	—		
		3–48	8.8	7.6	9.6	Very Light
		7–48	42.6	6.7		Medium
		12–48	38.1	5.5		Light

TABLE II.—Infections of Florida Oysters with *Nematopsis ostrearum* Compared with Condition Index and Mortality from Controlled Experiments at the Pensacola Laboratory (20 Oysters Used Each Month).

Month and Year	*Average Number of Cysts*	*Index of Condition*	*Mortality Monthly Av.*	*Intensity of Infection*
4–48	19.4	5.14	——	Light
5–48	——	6.18	3.5	——
6–48	10.5	4.26	16.8	Very light
7–48	41.2	3.71	30.4	Medium
8–48	64.1	3.21	21.7	Heavy
9–48	26.0	2.48	13.7	Light
10–48	29.4	2.61	17.3	Light
11–48	46.3	2.48	29.1	Medium
12–48	——	——	17.8	——
1–49	112.3	2.34	8.0	Very Heavy
2–49	21.1	2.95	3.4	Light
3–49	22.8	4.04	2.2	Light
4–49	25.9	4.98	2.2	Light

TABLE III.—Compilation of Results by Natural Drainage Areas of Louisiana; Data from Table I.

Area	*Month and Year*	*Av. No. Cysts per Sample*	*Index of Condition*	*Intensity of Infection*
I	10–47	62.5	——	Heavy
	3–48	43.9	8.8	Medium
	7–48	115.5	6.6	Very Heavy
	12–48	52.2	5.0	Medium
II	10–47	32.5	——	Light
	3–48	44.6	5.8	Medium
	7–48	100.3	7.9	Very Heavy
	12–48	59.1	4.5	Medium
III	10–47	26.5	——	Light
	3–48	31.5	10.4	Light
	7–48	34.2	5.6	Light
	12–48	38.9	7.7	Light
IV	10–47	32.5	——	Light
	3–48	38.6	8.2	Light
	7–48	51.4	4.8	Medium
	12–48	15.2	6.1	Very Light
V	10–47	18.2	——	Very Light
	3–48	14.9	6.8	Very Light
	7–48	49.1	5.5	Medium
	12–48	23.4	5.5	Light

TABLE IV.—Total Mortality and Infection Results from 30 Louisiana Stations Grouped by Natural Drainage Areas.

Area	*Total Oysters Examined*	*Infection*	*Mortality*	*Intensity*
I	171	58.5	15.2	Medium
II	160	56.3	18.5	Medium
III	217	30.9	41.6	Light
IV	75	29.3	22.6	Light
V	100	26.7	9.0	Light

DISCUSSION

Largely because of Prytherch's work, *N. ostrearum* was suspected of being one of the possible causes of poor condition and mortality of oysters. However, our data do not support the application of Prytherch's view to Louisiana oysters.

The condition or quality of oyster meats is determined by several factors, one of the most important being seasonal differences in temperature and the reproductive cycle. This Condition Index is expressed by the equation: $\text{C. I.} = \frac{100 \times \text{dry wt. (gr.)}}{\text{Vol. of Shell Cavity (cc)}}$.

On recovery from spawning, oysters in Area II (Table III) attained their peak of condition in July 1948 when the intensity of encysted *N. ostrearum* spores attained a simultaneous maximum. However, this was not the case in Areas I, III, IV, and V, where the condition of the oysters followed the usual seasonal pattern (C. I. high in winter and spring, low in summer) and where the intensity of *N. ostrearum* still reached its peak in July, except in Area III. Oysters from stations 7, 10, 16, 18, 22, 24, 25, and 25A showed good condition at the maximum of infection (Table I).

At Pensacola, the oysters examined came from among those held in concrete tanks. On examination of Table II, it will be seen that the same lack of correspondence between the intensity of *N. ostrearum* and Index of Condition prevails.

There have been two known cases where *N. ostrearum* has been reported as a causative agent for oyster mortalities (Prytherch, 1940; Southern Reporter, 1944). The inference has been drawn that heavy infection results in the physical impairment of the ostia or vascular system or of both, this resulting in debilitation and finally death. From our observations, occasionally there are extremely heavy infections that are detrimental to the health of the organism. However, because Areas I and II, both low mortality areas, show a significantly higher infection than does Area III, a high mortality area, it appears logical to conclude that the extensive mortalities can not be attributed to this organism (Table IV). Station 16 (Table I) clearly illustrates this point. Of the 295 dead oyster meats recovered from the experimental tanks at the Pensacola Laboratory, only four oysters had an abnormally high incidence of infection. The remaining oysters averaged 8.2 cysts per field, with a maximum of 132 and a minimum of zero. From these results it is apparent that there are other factors that cause the differential mortality.

Sprague (personal communication) has stated that "experimentally produced infections incomparably more intense than anything seen in

nature, using the two [*Nematopsis*] species separately, do not show conclusively that either one is particularly harmful to the oyster." Engle (1946) stated that no correlation could be found between distribution and intensity of infection of *Nematopsis* with poor condition and mortality in oysters of upper Chesapeake Bay.

The fact that histolysis surrounding spores was not observed in any infected tissues is additional evidence that eliminates *N. ostrearum* as a factor responsible for poor quality or mortality of oysters.

The spores found in the tissues are inactive, i. e., they do not reproduce within the body of the oyster. The outer wall of the cyst is laid down as a result of the tissue reaction of the host organism. There is no evidence of a continued irritation response. This, of course, does not eliminate the potential pathogenic effect which might result from migrating larvae before phagocytosis occurs.

It is significant, however, that the intensity of infection increases during the summer months. In contrast to Area III, Areas I, II, IV, and V of Louisiana and the Pensacola Station illustrate this seasonal variation. No positive reasons for the variation can be offered other than ecological differences from one area to another. One could postulate variation in intensity as a function of distribution of the definitive host and concentrations of gymnospores in the water, but there are no data available for this.

The intensity of infection is generally considered to be a function of the age of the oyster, the older oysters generally having the larger number of cysts. However, some individuals of obvious old age were comparatively free of the parasite, although they were found in a community of high incidence of infestation. This fact, plus the seasonal fluctuation in infections, warrants our calling attention to the possibility that the oyster resists the infection or is able to eliminate the encysted spores, or both.

CONCLUSIONS

1. Based on representative samples over a period of two years (1947–1948), oysters from the major producing area of Louisiana were found to be 100% infected with the gregarine parasite *Nematopsis ostrearum*. Oysters from Pensacola Bay, Florida, were found to be 95.1% infected.

2. In Louisiana, the population of *N. ostrearum* was found to be higher in the area known as the "Louisiana Marsh," which is located east of the Mississippi River.

3. *N. ostrearum* infections in oysters increased significantly during the summer months in the lower mortality areas of Louisiana and at Pensacola, Florida.

4. *N. ostrearum* is not the controlling factor which is responsible for the Index of Condition of oysters or for the extensive mortalities of Louisiana oysters.

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THE ESTIMATION OF DISSOLVED PHOSPHATE IN SEA WATER[1,2]

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ABSTRACT

The molybdenum-blue method of determining dissolved inorganic phosphorus in sea water was modified for use with a photoelectric colorimeter. The effect of reagent concentration, time, and temperature on the rate and extent of color development was studied. Practical suggestions are given for carrying out routine analyses at sea.

INTRODUCTION

The molybdenum-blue method for determination of dissolved inorganic phosphorus in sea water has been in use for many years. Modifications have been made in the conditions of analysis (size of sample, reagent concentration, time of standing, and temperature) and in the methods of making the colorimetric comparison of standard and unknown samples.

In recent years attempts have been made to adapt the method for use with photoelectric colorimeters. Harvey (1948) has made a careful study of the method with a photoelectric colorimeter of his own design.

In 1948 it became evident that work of the Marine Life Research program of the Scripps Institution of Oceanography would require that large numbers of routine phosphate determinations be carried out at sea by semiskilled personnel. A preliminary study showed that further modification of the method and a better understanding of the effect of various factors on the reaction would be required in order that data obtained by various people on different ships be consistent and reliable. This paper presents the results of this work on the phosphate method, carried out during the last two years.

Absorptimetric terms and symbols used are those adopted by the National Bureau of Standards and described in Letter Circular LC-857 of the National Bureau of Standards (1947).

APPARATUS

All spectrophotometric measurements were made in a Beckman Model DU Quartz Spectrophotometer with 10-cm absorption cells having Corex windows. Certain photometric estimations of phos-

[1] This work has been supported by the Marine Research Committee of the State of California.

[2] Contribution New Series No. 517 from the Scripps Institution of Oceanography.

phate were also made in a photoelectric colorimeter, the Automatic Servo-operated Photometer (ASOP) to be described elsewhere. In this instrument monochromatic light was obtained with interference-type filters peaked at a wavelength of 700 mμ;[3] 10-cm absorption cells were used, the instrument usually being balanced against an air light-path rather than against an absorption cell filled with the solvent. A correction was applied for absorbancy of the cell and solvent.

Reagents were added either from micro-burets or from specially designed reagent dispensers to be described elsewhere.

FORMATION OF MOLYBDENUM-BLUE

Addition of a small quantity of a sulfuric acid solution of ammonium molybdate to a sample of water containing phosphate ions results in formation of a phosphomolybdate complex. Subsequent reduction with an acid solution of stannous chloride produces a blue color, the intensity of which varies with the concentration of phosphate ions initially present. The rate at which color forms and then fades and the intensity of the color formed depend also on the concentration of reagents and on the temperature and salinity of the sample.

Robinson and Wirth (1935), using either Atkins or Truog-Meyer reagents, found that the maximum intensity of color occurred seven minutes after addition of reagents, but they observed no fading until after an hour. More recently, Robinson and Thompson (1948) found that the maximum color intensity developed in about seven minutes, but they made no statement about duration of this maximum intensity.

In this laboratory, the formation of molybdenum-blue was studied by adding reagents to a sample and by transferring the sample to an absorption cell which was immediately placed in the spectrophotometer. Readings of transmittancy were made at frequent intervals; during intervals when readings were not being made, the absorption cell was out of the light path and hence in the dark. In a study of the reagents used by Wattenberg (1937), essentially the same as those employed by Robinson and Thompson (1948), it was found that in sea water color developed within 5 minutes to within 2% of maximum absorbancy, remained within 2% for about 10 minutes, then faded.

It was desirable to extend the flat part of the curve so that large numbers of samples could be analyzed efficiently at sea. Harvey (1948) showed that adding increased quantities of stannous chloride increased the rapidity of color development, delayed the onset of

[3] Although Harvey (1948) states that the blue substance produced in distilled water has a different light absorption band from that produced in sea water, the absorption spectrum studied with the spectrophotometer showed peak absorbancy at 700 mμ in distilled water, in 3.3% NaCl solution, and in sea water.

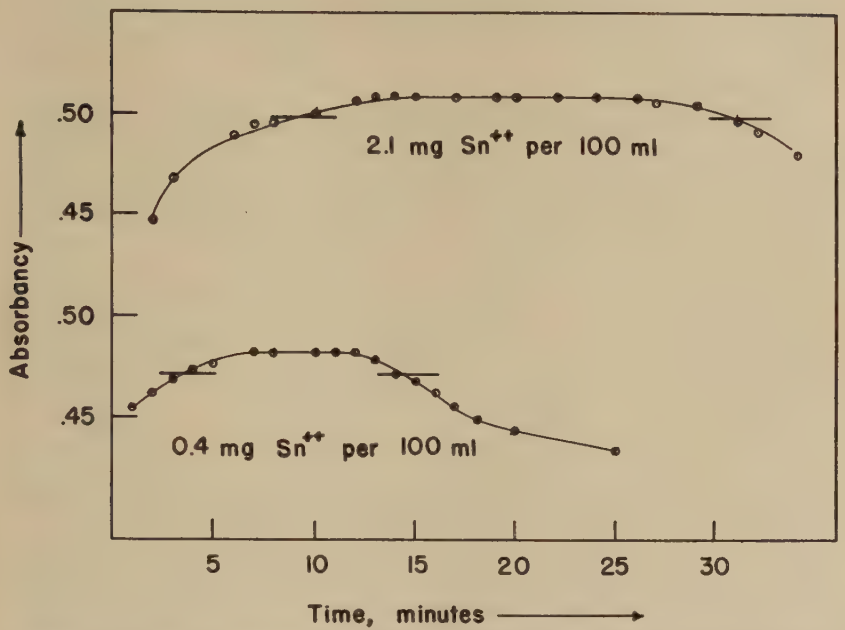

Figure 1. Effect of concentration of stannous tin on stability of molybdenum-blue. Samples are sea water with 1.5 μg at/L of added PO_4-P.

fading, and increased the amount of color formed with a given quantity of phosphate. He used concentrations of 0.43 to 0.64 mg Sn^{++} per 100 ml of sample; most workers have used concentrations approximating these.

The maximum practicable tin concentration seems to be about 2.1 mg Sn^{++} per 100 ml sample; upon further increase, reagent blanks develop a colloidal precipitate of tin oxides and are unreadable. With this concentration of tin, color develops within 10 minutes to within 2% of maximum absorbancy and remains within 2% for 20 minutes (Fig. 1). With such a long period of time during which the absorbancy remains constant, it is possible to make large numbers of determinations rapidly, scheduling additions of reagents and readings of absorbancy without waste of time.

Objection has been raised to increased tin concentration on the grounds that a yellow coloration appears and interferes with readings. This color is evident particularly with low phosphate concentrations and with the long absorption paths customarily employed in visual colorimetry. When measurements are made at the peak absorbancy

(700 mμ) in a photoelectric colorimeter there is no evidence of interference. Linearity of standardization curves with this tin concentration is evidence that the discoloration, if present, does not interfere with accuracy.

In addition to an increase in the period of time during which readings can be made, an increase in the tin concentration increases the sensitivity of the method. However, this increase is not as great as that resulting from an increase in the absorption cell length from 10 cm to 15 cm.

TABLE I.—Effect of Medium on Duration of Maximum Absorbancy

Concentration added PO_4-P	*Duration of maximum absorbancy**		
	Dist. water	*3.3%NaCl*	*Sea water*
μg at L	Min.	Min.	Min.
0.6	6–19.5	7–32	9–31
3.0	1– 8.5	6–17	8–26

* Time after addition of reagents during which absorbancy is within 2% of its maximum value. Sea water salinity approximately 33 °/₀₀.

The rate of color formation and the amount of color formed are also affected by the phosphate content and by the salinity of the sample. Maximum absorbancy is attained more slowly and persists longer in samples with low phosphate content. However, if color is considered constant while it is within 2% of maximum absorbancy, it is found that, in sea water, color is constant at all but the highest concentrations of phosphate (greater than 2.4 μg at/L) from 10 minutes until 30 minutes after reagents are added. At higher phosphate concentrations, color is constant only until 25 minutes after reagents are added.

When reagents are added to either distilled water or to a 3.3% sodium chloride solution containing added phosphate, the rate of color formation is much more sensitive to phosphate content than is that of a sea water dilution (see Table I). The molybdenum-blue color is more stable in sea water than in either salt solution or distilled water.

The rate of color development and the amount of color formed are also affected by the temperature of the sample. At a lower temperature, maximum absorbancy is not attained so rapidly and is not so great as that at a higher temperature. Thus, as temperature increases, the slope of the standardization curve, hence the sensitivity of the method, increases.

If a series of standardization curves is run at different temperatures and if the absorbancy index of each curve is plotted as a function of temperature, it is found that the absorbancy index varies linearly with

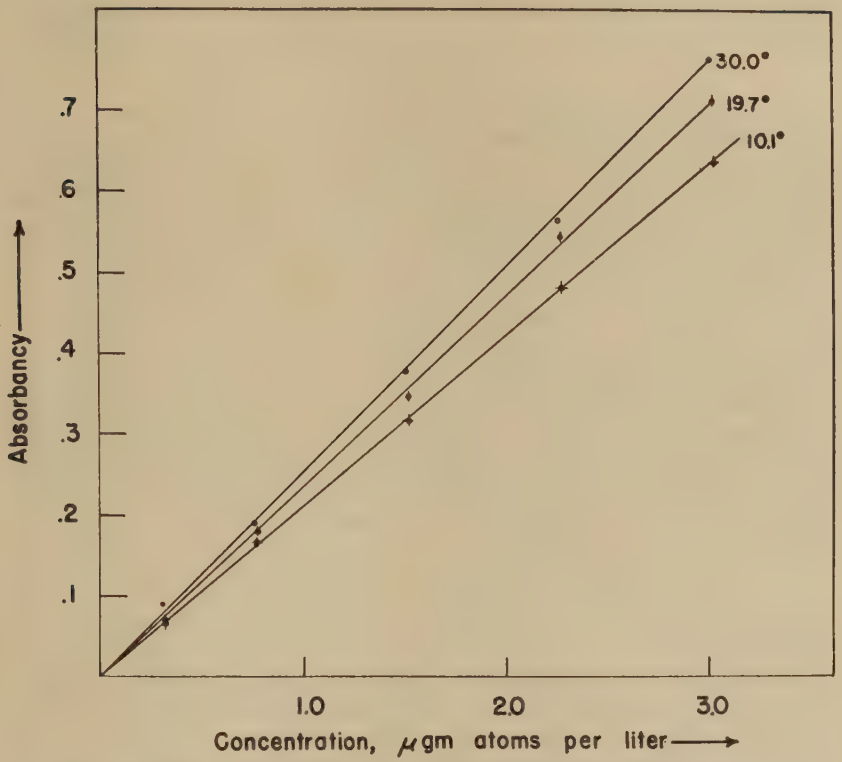

Figure 2. Phosphate standard curves at various temperatures, using sea water with added phosphate. These curves have been passed through the origin to emphasize the change in slope.

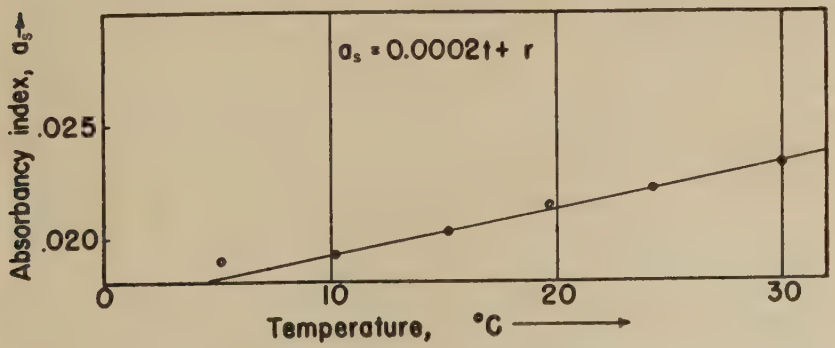

Figure 3. Absorbancy index as a function of temperature.

temperature between 10° and 30° (Figs. 2 and 3). The equation of this function is:

$$a_s = 0.0002\, t + r,$$

where a_s is the absorbancy index, t the temperature in degrees centigrade, and r the residual constant.

Previous workers have found an apparent change of concentration of about 1% per degree temperature difference between the temperature of standards and of unknown samples. Calculations based on the above equation are in agreement with these observations.

If a constant temperature bath is available it is obviously best to bring both standard and unknown samples to the same temperature before analysis. An alternate method is to measure the equilibrium temperature of unknown samples and to apply a temperature correction, using the above equation. In the latter method there is the disadvantage that six hours may be required for samples from deep stations to reach an equilibrium temperature, during which time the phosphate content may change significantly. In a water bath, on the other hand, samples can be brought to temperature in ten minutes or less.

PREPARATION OF REAGENTS

Molybdic Acid: Dilute reagent-grade sulfuric acid with an equal volume of distilled water and cool to room temperature. Mix 3 volumes of this dilute sulfuric acid with 1 volume of molybdate solution containing 10 gm of ammonium molybdate $[(NH_4)_6Mo_7O_{24}\cdot 4H_2O]$ per 100 ml distilled water. Molybdic acid solution should be stored in a dark bottle and should not be allowed to come in contact with rubber.

Stannous Chloride: Place 2.1 gm of granular tin metal (reagent grade 20 or 30 mesh) in a small beaker and add 22 ml of reagent-grade hydrochloric acid. After solution is complete, usually in 3–4 hours, dilute to 200 ml with distilled water. Add several pieces of mossy tin and store under paraffin oil.

Standard Phosphate: A stock solution containing 3000 μg at. of added PO_4-P per liter is prepared by diluting 0.408 gm of reagent-grade KH_2PO_4 to 1000 ml with distilled water. Several drops of chloroform are added as a preservative. A working solution, containing 30 μg at. of added PO_4-P per liter, is prepared by diluting 10 ml of the stock solution to 1000 ml with low-phosphate sea water (surface water obtained away from the coast). This low-phosphate sea water ordinarily contains from 0.3 to 0.6 μg at/L of phosphate-phosphorus. It is not essential that these standards contain exactly their nominal phosphate content if subsequent dilutions are made accurately, since, in standardization, the *slope* of the curve, absorbancy

vs concentration, is required rather than the *absolute value* of absorbancy for each concentration.

METHOD OF ANALYSIS

Measure duplicate 100-ml samples for analysis (see *Notes 1 and 2*), including duplicate 100-ml samples of distilled water for reagent blanks. Bring the samples to a known temperature or measure the temperatures of representative samples. To each sample add 1.0 ml of molybdic acid solution, shake thoroughly, and add 0.2 ml of stannous

Figure 4. Phosphate sampling bottle. Dimensions of plug depend on volume of bottle used

chloride solution (see *Note 3*). After shaking thoroughly, record time of reagent addition. At least 10 minutes, but not more than 25 minutes, after addition of reagents, measure absorbancy of samples and reagent blanks at 700 mμ in a 10-cm absorption cell (see *Note 4*).

In order to relate absorbancy to concentration, 3 or 4 standard curves are determined for each batch of reagents. A series of dilutions of standard phosphate solution is made with low-phosphate sea water and these are analyzed as described above. Absorbancy is plotted as a function of concentration and the slope of the curve is determined. The given equation is used to determine the magnitude of the temperature correction. Absorbancy of the reagent blank is subtracted from absorbancy of the sample; the remaining absorbancy is divided by the product of absorbancy index, a_s, and the cell length, l, to give the concentration of phosphate-phosphorus.

Note 1: Smaller samples may be used if a small-volume absorption cell is used, but they must be measured with greater accuracy. If 50-ml samples are used, reagent quantities given should be halved.

Note 2: Samples can be drawn conveniently and accurately in the sampling bottle shown in Fig. 4. The bottle, although it contains a

volume somewhat greater than 100 ml, is closed by a loose-fitting brass plug with dimensions such that it will displace sufficient water so that the bottle will deliver 100 ml (precision of about ± 0.5 ml) when the plug is removed.

Note 3: Molybdic acid solution should not be pipetted from a stock reagent bottle because of the danger of contamination. If a buret is used, it must be remembered that molybdic acid solution turns blue on prolonged exposure to light or in contact with rubber. Similarly, stannous chloride solution is readily oxidized when exposed to air. Specially designed reagent dispensers are convenient for precise addition of reagents at sea.

Note 4: Absorption cell windows are gradually stained upon repeated exposure to solutions containing molybdenum-blue. This stain can be removed by filling the cell with a 10% solution of hydrofluoric acid and allowing it to stand for 15 minutes. The extent of this staining and its effect on the absorbancy of samples can be determined by measuring the absorbancy of the cell filled with distilled water, after first balancing the photometer for 100% transmittancy through an air light-path. If such cell checks are made before and after each group of determinations, it is possible to correct for the absorbancy of the cell itself. Then absorbancies of samples can be measured relative to an air light-path rather than relative to a cell filled with water.

RANGE AND ACCURACY OF METHOD

Ayres (1949) showed the value of plotting "absorbtancy" (100 minus transmittancy) against log concentration in studying range and accuracy of a photometric analytical method. He showed, on theoretical grounds, that the straight line portion of this curve reveals the optimum range of the method and that the slope of this line is a measure of the relative analytical error. The optimum range is a function of the wave length used, and the relative error is a function of the concentration of substance being studied.

Such a study of the method described above shows that, when photometric readings are made at 700 mμ in 10-cm absorption cells, the optimum range is from 1.0 to 3.5 μg at. P/L. Although Beers Law seems to obtain down to the very low concentrations, the relative error is greater below 1.0 μg at/L. In a typical curve, shown in Fig. 5, the relative analytical error in the optimum range is 2.8% per 1% photometric error. Between 0.4 and 0.8 μg at/L, however, it is 4.7%. Since the photometric reading error may be reduced to about 0.2%, the relative analytical error becomes only a fifth of these values, or less than 1% in both cases.

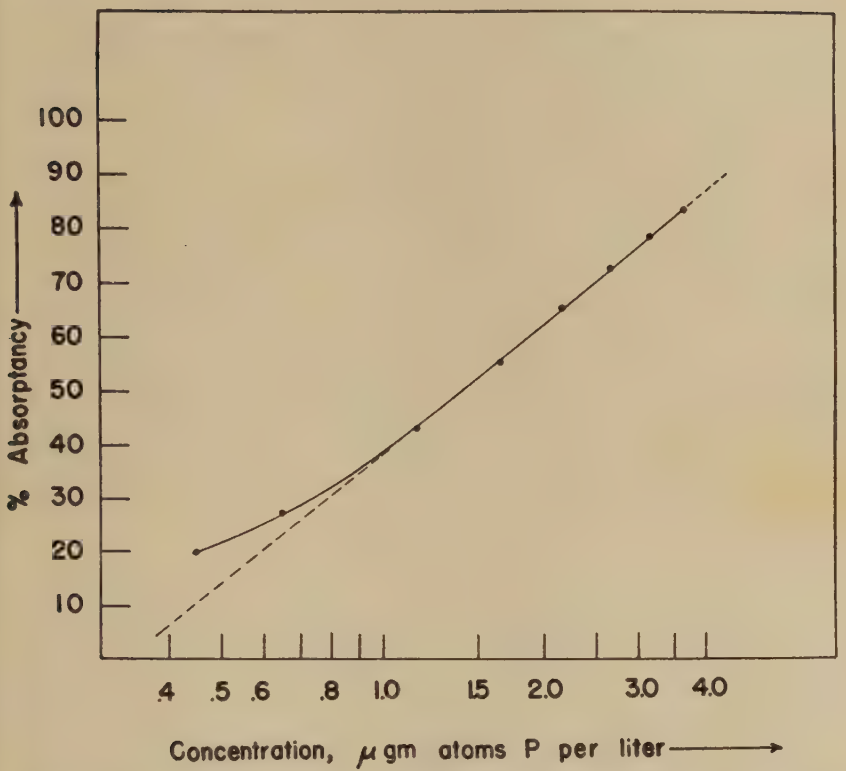

Figure 5. Curve for estimating optimum range and accuracy, according to method of Ayres (1949). Sea water at 10.1°, measured on 10-cm absorption cells at a wave-length of 700 mμ.

There are other important sources of error not treated by Ayres' method. These include sampling errors, error in determining the relation between absorbancy and concentration, and error in determining reagent blank. The presence of certain of these errors, in addition to those inherent in visual colorimetry, makes one question the usual estimates of 5 to 10% accuracy for the traditional method. Although the precision of measurements made by the method described above is usually better than 2% of concentration, the accuracy at the present time cannot be said to exceed 5%.

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AN ATTITUDE ON "FISHERY HYDROGRAPHY"[1]

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[An essay on the theme that the fortunes of North Sea fish broods *may* be determined by some factor (or by some complex of factors) resident within those broad features of water circulation which are ruled by widespread wind conditions inferable from the study of atmospheric pressure gradients, followed thereafter by an ADDENDUM (due to Günter Dietrich) dealing with month-by-month wind conditions over the northern North Sea during the half century now ending, and by an ADDENDUM NOTE briefly indicating what progress has been made along the lines concerned and what is in prospect.]

INTRODUCTION

This essay was written on learning that particular attention would be paid to Fishery Hydrography at the 1950 reunion of the International Council for the Exploration of the Sea. It happened that the writer and his colleagues had just finished preparing a series of papers dealing with the close inter-relationship of wind and water movement. For that work, several special tabulations of wind conditions had been commissioned, these tabulations being of a type quite novel in some respects. Since the first of these to come to hand dealt with the northern North Sea area, it was decided to apply it in an attempt to carry further (in respect of haddock) what had been started in 1938 when a first attempt was made to find correlations between brood-strength fluctuations of that fish and wind conditions.[2]

The paper then written was entitled: *Fluctuations in the herrings of the East Anglian autumn fishery, the yield of the Ostend spent herring*

[1] This paper is published with the approval of the Lords Commissioners of the Admiralty, but the responsibility for any statements of facts or opinions expressed rests solely with the author.

The essay was placed before the Northern North Sea Committee of the International Council for the Exploration of the Sea during its 38th annual reunion held in Copenhagen in October 1950. On that occasion, its content was summarized in lecture form by the author, and it was debated in concert with other themes within the general field of "Fishery Hydrography," which topic will be much to the fore at the 1951 reunion of the Council.

[2] Rapp. Cons. Explor. Mer, *107* (III, 2), pp. 10–15, 1938.

fishery, and the haddock of the North Sea—in the light of relevant wind conditions. Considering that the results then obtained in respect of haddock were of promise, the following steps were decided upon when the topic was reopened in 1950:—

1. To write the following essay so that the basic belief could be adequately set down on paper. This belief is that wind rules water to a degree which compels the thought that fish fortunes can hardly fail to be dependent in large measure upon wind conditions.
2. To put into the hands of other workers in the field of fishery research certain new presentations of wind conditions over a goodly term of years, thus enabling them to seek causative linkages in their own special spheres of interest should they so wish. Of these new wind presentations, that which is the subject of the ADDENDUM (p. 113) is the first.
3. To put the general thesis of this essay to the test by applying it in a study of fish fluctuations (see ADDENDUM NOTE, p. 116).

Because the northern North Sea was initially concerned, the writer naturally decided to turn first to the haddock. Considering that a new approach by persons fresh to the subject might well prove profitable, he briefed his colleagues in the Admiralty and gave them a free rein with the wind data and all the *published* haddock data on brood strength variations which he could find. By so doing it came about that adequate mathematics was applied. If results proved promising enough, the idea was to make application to the Director of the Scottish Home Department's marine laboratory at Aberdeen to have the matter taken over by B. B. Parrish, who would be able to bring to it the requisite full knowledge from the haddock side. When the present essay was placed before the Northern North Sea Committee (thanks to the good offices of C. E. Lucas), placed with it was a report by Parrish setting out what had come from the collaborative effort of all concerned in the matter of associating haddock fortunes and wind conditions.

"Hydrography" and "Hydrographer." We shall here invest these two words with the connotation accepted in International Council circles, although the word "Hydrographer" in Britain and the U. S. A. customarily attaches to one person only and has a long-standing meaning accordingly. Much discussion around these terms can be found in early issues of the International Hydrographic Review published from Monaco.

By "Fishery Hydrography" we mean those studies of water conditions which are devoted *mostly,* though not exclusively, to the aim of

explaining why the spawning products of different years produce such different accessions to the stocks of adult fish some years later. Sight is not lost of the necessity to establish by proper investigations whether or not the stocks of adult fish in the sea *were* better in one year than another.

In the following essay we shall use the expressions "Water Events" and "Fish Events" with obvious meaning to avoid some needless repetitions.

Those who read this essay will be able to accuse the writer of assailing his own cloth; they may not infer, however, that he necessarily regards the house of the nonhydrographers as completely in order. Snobbery is rife in science, as in so many other walks of life, and the writer has no great confidence that the simple line of work he urges below will make any solid appeal. If there were real likelihood of it doing so, there would have been some reaction earlier to a paper in which he said so much along similar lines.[3]

It does seem to be the case that interest is always aroused by, and support ever forthcoming for, grandiose plans of work which require impressive paraphernalia with provision of much gear, many workers, and lots of money.

Cinderella has little chance in the beauty chorus of modern research, but the writer is entirely sincere in what he advocates, because he feels convinced that only the wide view holds any real promise in Fishery Hydrography. With such a vast and unruly thing as the sea to deal with, who shall say of fisheries research that the day of "bits of string and bits of wire" has completely passed, and that the ball now lies only at the feet of the smart scientist with his plethora of gadgets?

GENERAL DISCUSSION

Fishery research literature abounds with discussions of what *may* have determinative influence upon the upgrowth of spawning products, and numerous papers could be cited with ease which deal with different aspects of the brood survival problem. It would seem that there is a risk of forgetting that relevant studies of very real merit were made quite a long time ago. That this is so emphasizes all the more the need to pause a while to take stock and assess what progress has been made to date.

An address given by A. T. Masterman before the British Association as long ago as September 1896[4] would be no bad starting point for a

[3] *Carruthers, J. N.* Practical proposals for a continuous programme of thick-layer current measuring in all weathers with remarks on relevant wind observations and other related matters. J. Cons. int. Explor. Mer, *15* (1), pp. 13–26, 1947.

[4] Natural Science, Vol. 10, (64) June 1897.

man who might attempt to lay out the task facing a Fishery Hydrographer who aimed to associate water conditions and fish fortunes with a view to discovering anything of real elucidative value in the former. As far back as 1864, G. O. Sars, who recorded instances in which adverse currents had "beached" myriads of cod eggs to form a long glistening line at high tide, was speculating upon the possible effect of such destruction of spawning products. Strangely enough, there seems to be no record of observations that plaice eggs from the great spawnings in the southern North Sea have ever been beached. In 1893, C. G. Petersen was devoting much thought to the part played by physical conditions upon larval fish which supposedly need to reach waters near shore "at the right time" to find satisfactory survival conditions. Fulton, Hjort, Dannevig and others were no less alive to the importance of studying water conditions such as temperature, saltness, currents, etc. in connection with the dispersal of products of spawning, and they adduced ideas as to what was adverse and what optimal.

In the early paper by Masterman, just cited, there was already talk of the voracious gobbling of herring ova by haddocks. As will be known to all who may read this essay, that habit has been considered by some people to be a possible, if no more than a partial, explanation of the surprising "oppositeness" of good haddock years and good herring years. If the linkage *is* a feeding one, obviously it can operate only if the voracious young haddock occur where the herring ova are present. The existence of this situation can be quite well understood from lines of argument developed by the present writer in an earlier paper, and which are implicit in what follows.

The citations given above from writings of early days, antedating the establishment of the International Council, have a deliberate purpose. Surely, the work done in the ensuing 50 years of the Council's existence does justify the stand taken by those who would now call upon the hydrographers for a "stocktaking," so to speak. Nothing said in what follows implies that the writer holds hydrography to be a less important concern of the Council than is fisheries biology, but it is only fair to admit that we hydrographers who assemble periodically in Copenhagen should now declare where we have gotten and how we propose to direct our steps in the future.

We have a *special* job to do.

In marine laboratories not specifically charged with Fishery Hydrography and not State-financed to that end, all researches, no matter what their description or potential usefulness, are fully justified as strivings after knowledge of the sea. In those institutions which have fish problems as their major *raison d'être*, however, there must surely

be some particular and less-dispersed attention to lines of work which, on *a priori* grounds, would appear promising.

Here the writer fully realizes that he courts rebuke on the grounds that such doctrine is "unscientific," for who shall say that the most unlikely researches might not reveal the answers to the problems? The history of science is rich in showing that important discoveries have emerged from investigations in no wise deliberately steered. These things are fully realized, and nothing is further from the writer's wish than that meticulous researches on plankton, on phosphates, on silicates, and on a host of other factors, should in any way slow up or be discouraged. Admittedly, from them might well come the answer to important problems in Fishery Hydrography, but there are certain serious practical considerations to face.

With the passage of each year the mountain of data gets ever bigger, and the hydrographers insist on more and more details. Their requirements in the field of sampling become ever closer, their consumption of ships' time becomes ever more extensive, their call upon the help of analysts becomes ever more serious, the cost of their investigations becomes ever more expensive, and their lists of published data become ever more formidable. As the poet Burns so pertinently remarks: "Facts are chiels that winna ding and downa be disputit . . ." and we must face them.

It is in no sense a question of "selling the pass" if one hydrographer declares himself somewhat in sympathy with the disquietude of the International Council's Executive over the situation.

Just before World War II, a situation had come about wherein that body was beginning to take a stand which might be put more or less in the following words:—

> We have every sympathy with what the hydrographers tell us it is necessary to do; we have no lack of appreciation of their stated needs for greater density of stations and detail of sampling, and we realize that such an increase of work will naturally require more and more pages in the Bulletin Hydrographique. Yet, the time has come to ask ourselves whether greater charges on time, on ships' effort, and on money and printing can be afforded.

To dwell upon such matters is to concern oneself with things which are not science, but it does no good to reject them as absurd. At this stage it is well for hydrographers to claim acquaintance with various ideas put forward in numerous papers over past years regarding those supposed linkages between water events and fish events wherein *may* lie fish survival explanations.

We recall the importance with which the question of dispersal of eggs and early stages has been invested; must young stages be trans-

ported to certain areas within a critical time in order to experience good survival? We recall too, the idea that there must be adequate planktonic food at about the time when young fish pass the yolk-sac stage. We are not unaware of the importance supposedly attached to the habit of some fish to move off contranatantly to spawn. Known to us also is the alleged importance of barriers in the sea consisting of those masses of noxious plankton which are supposed to be responsible for obstructing the movements of, or deciding the distribution of, herring. We are also aware that adult fish, enfeebled by spawning, may be more or less passively transported by currents.

Questions of upwelling, of cascading, of shifts (horizontally and vertically) in the position of thermoclines, of nutrient-poor and nutrient-rich water, of the formation and movements of slicks and of convergences and divergences, of types of bottom, of strengths of current, of lethal salinities, of comfortable temperatures, and of many other things, are, it is hoped, sufficiently within our ken to warrant our topical attention. All of these will be borne in mind, and we shall think also of such things as Hodgson's views on the response of adult clupeoids to wind (opposite for herrings and pilchards).

Although no Fishery Hydrographer ought to be ignorant of those numerous divisions of the field of fisheries research in which many of his fellow investigators must work, our present point is that a few of his kind ought to ignore them *pro tem*, as problems needing specific attention, and ought to try first a broad simple approach on lines comprehending them all at once, more or less. That may sound like extravagant over-simplification, we freely admit, but it is hard to suppose that the pronounced modifications of water circulation which are produced by the winds' influence can be without marked effect on important fish events in the North Sea.

By no means have we set down all of the water events which could be taken into account in some measure by devoting attention to water movements indirectly via the consideration of wind conditions inferred from atmospheric pressure data. There is a whole string of water events which depends upon the outflow from the Skagerrak. Fluctuations in the strength, width, and volume of the north-going surface current up the coast of Norway do so depend, and, in turn, so does the distribution of water characteristics produced by them.

In recent years, ways have been worked out to forecast the water movements through the Danish waterways, and interconnections have been established between Baltic-to-North Sea currents and barometric pressure distributions.

We think that these and earlier remarks strongly support our advocacy of what is urged below.

A POSSIBLE SHORT CUT

Part 1. Observations on Currents. Whatever factor, or complex of factors, may be responsible for exerting determinative influence upon the products of spawning, i. e., whatever it may be which spells good or bad augury for fish broods, one can reasonably expect that it will be taken account of by (because comprehended within) an adequate consideration of water movements. Whatever chemical, physical, or planktonological conditions may be critical, such will necessarily be in a state of space flux dependent upon currents. That seems reasonable enough, and to make the requisite study of currents would amount to devoting attention to something much more widely embracing than any one line of detailed research concerning some one specific factor, in as much as so many things would be included. In what follows, it is fully realized that arguments will suffer some loss of force from the facts that the writer will inevitably be "pushing his own wares," will be advancing proposals likely to be attractive to the "Powers that Be," and in general will perhaps be displaying himself as "unscientific."

This is all freely accepted.

To seek "explanations" of fish fluctuations and attendant matters good for the North Sea, it is urged that as good a way as any would be found in a programme of *continuous* current observations at as many places as possible. Means exist whereby it could be learned, for all days of all months, year after year, how the water had moved past all lightships in the North Sea. There is nothing fanciful about this at all; there is no maybe about it in the least. It could certainly be done.

The aim would be to have a synoptic picture of the water movements that would be good for all time, and, if salinity or plankton (or something else) proved to be the factor that really mattered, then the distribution of that factor would automatically be taken account of without thinking of it specifically. Just before World War II there had been a considerable approach to what is now urged. At ten light vessels such a programme was in being. The necessary apparatus exists, and the cost to run such a programme, with the instrument possessed, would be about £ 90 a year per ship, according to present British experience. Papers published in the Council's *Rapports et Procès-Verbaux* just before the war (when the present writer was "Recorder on Currents" to the Southern North Sea Committee) show the way in which things were then moving in this connection.

Since those days means have been provided whereby gaps could be filled in for areas in which no lightships are moored. With the "rough and ready" current-measuring instrument as a means to the results

given in those *R. et P.-V.* papers, one had in being a programme of continuous observations of water movements which let the results be known with great speed.

There was no awkward piling-up of data; all one really needed to know about the water movements over a whole year at a number of places could be set down in very little space in a printed report. If so wished, the results could be collected at sea almost immediately after observations had been taken. This was customarily done by having the records floated out to a visiting ship in a watertight tin veered away from the lightship at the end of a casting line.

Working along lines now urged, one could later set down, in very modest printed space, the information on water movements for many places (*without breaks in continuity caused by wild weather*) which would serve for application to studies of fish events. That there need be no waiting and no gaps in the data is amply attested by past experience. There is no serious expense; there is no consumption of research vessel time; there is next to no call upon the time of scientists; and there is no ponderous analysis to be done before the information on water movements is available for use in the fish connection.

The information accruing from a programme of continuous current observations such as is here advocated is not limited in usefulness to fishery research workers; it also has solid value to physicists studying storm surges, to engineers concerned with coast erosion, to climatologists, to sedimentary petrologists, and to persons concerned with navigational matters. These other interests could doubtless be drawn in to help with the modest expense.

Part 2. Currents via Wind. Just before the war the writer of this essay had thought it a good idea to go even further to determine whether the practitioner of Fishery Hydrography could possibly get information of elucidatory value in the fish connection from a line of work even simpler, much more widely embracing, and cheaper to the point of nearly no cost at all. This he did by turning to the consideration of widespread wind conditions as inferred from a study of barometric pressure gradients. This step had not been taken until it had been sufficiently established that wind rules water to a very profound degree over the North Sea and adjacent regions. For instance, at the position of the Sandettie Lightship, a place important in several fish connections, it was found that a thick surface layer of water moves averagely 13.2 miles northeastward and 11.6 miles southwestward in the course of a day (a net flow of 1.6 miles per day towards the northeast). Records show that, under certain wind conditions, the respective flows have been 4.9 and 20.3, evidencing a net travel of 15.4 miles

in the day towards the southwest. Still thinking of a thick surface layer of water (which could, within reason, be as thick as desired) and of water travel within a day, it may be added that the water at the position of the North Goodwin Lightship has been known to move 13.5 miles over-all per day towards the southwest on one occasion, and 10.5 miles towards the northeast on another. At a position within the Thames estuary (here the thought of manurial salts discharging into the sea comes to mind) the extremes *can* be as much as 10.2 and as little as 4 miles seawards.

As far back as 1874, William Ferrel derived the relation between the barometric gradient and the velocity of the wind, so we may read, but even before that, in 1868, people in Britain were already plotting barometric gradients over the North Sea and working out the strengths and directions of wind implied by such gradients. It was Thomas Stevenson in 1867 who first used the expression "Barometric Gradient," and in those days it was remarked that a gradient of "0.02 inches of mercury per 15 miles, indicates the probability of as much wind as an ordinary yachtsman likes to meet with." In those early days we find the interested persons calculating winds of different speeds and of various directions over the North Sea from the directions of gradients, and we read that they standardized the statements for separation distances of 100 miles.

It is interesting historically to set down these facts, since one of the author's chief concerns here is to emphasize the length of time over which people have been busy on questions which have such present day interest, thereby giving weight accordingly to the plea that a stock-taking is now amply called for.

If it can be shown that fish events of interest to the Council (be they in connection with newly-spawned eggs and young larvae or with enfeebled shotten fish) and of concern to the practitioners of Fishery Hydrography are correlated with the broad water movement features of the North Sea inferable from barometric pressure gradients, some progress of value will undoubtedly have been made. In such a happy case we could handle barometric pressure data directly as though they were indicative of currents, and we should be in a position to go far with no expenditure of money to matter. The writer urges the doing of work along the lines here indicated on the grounds that it is reasonable and requires next to no expenditure of money.

More than that! We have to realize that we could never extend *any* programme of actual continuous current measuring to the deep and wide waters of the northern North Sea. There are means which could serve at great expense and trouble to give us data for which we should not have to wait, but they would not serve us adequately.

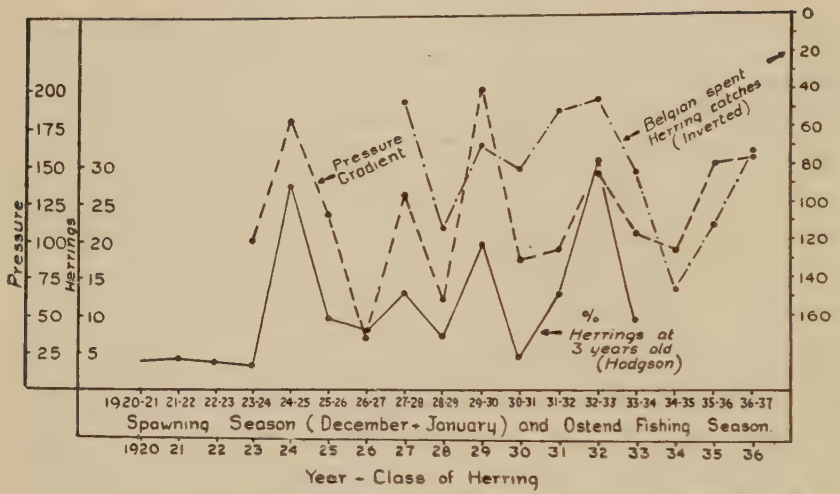

Figure 1. Yearly fluctuations in herring of the East Anglian autumn fishery and in the yield of the Belgian spent herring fishery compared graphically with yearly fluctuations in the atmospheric pressure gradient controlling the run of wind northwards up the Southern Bight during December and January. (Of the two scales on the left, the outer one gives the atmospheric pressure gradient and the inner one the percentage occurrence of herrings at three years old in the East Anglian catches. The inverted scale on the right refers to the yield of the Belgian spent herring fishery; values × 100 give in kilograms Gilson's mean weight of a day's capture.)

There is good reason to think that major fish events in the North Sea may well be decided by water events *within* that sea; at any rate, when the present writer was studying Graham's data on cod-brood strengths, with the great advantage of help from Sir Gilbert Walker, there seemed to be obtainable no suggestion of correlation with meteorological events over the Atlantic.

Before moving to the finish of this essay, a remark concerning the herring of the southern North Sea should be made. There seems never to have been enough thought given to the possible effects of *catastrophes*. Years ago, the writer questioned the sense of straining after explanations of good and bad years *via* the consideration of what could possibly be only minor influences without first giving due weight to the thought that one bad gale might destroy large areas of ova in the Cap d'Antifer region by siltation. A number of bad gales spread over the spawning season might reasonably be expected to spell bad augury. Now it is one feature of the proposed line of study through atmospheric pressure gradients that such catastrophes would be taken account of.

The fact that Lumby in Lowestoft is paying close attention to meteorology in the field of Fishery Hydrography, and doing so in a

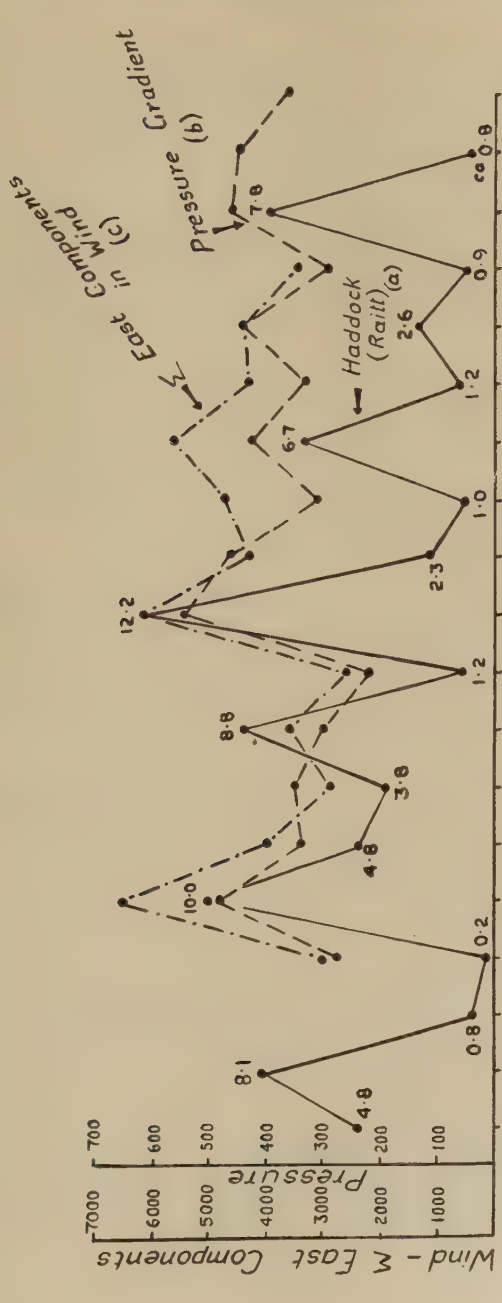

Figure 2. Showing (a) Raitt's curve of the relative numerical values of North Sea haddock broods in the first year of life, 1919–1936, (b) a curve portraying pressure gradient values from the SE quadrant during March, April and May, and (c) a curve relating to "East in the Wind" as computed from observations during February, March, April and May at three appropriate stations.

way good for a very extensive area (stretching far to the north), is to be heartily applauded. There seem to be grounds for hoping that fish events will receive some elucidation from the data he is so laboriously compiling. If they do not, the present writer feels but mildly optimistic of getting at any useful explanations otherhow.

An accompanying pair of figures (Figs. 1 and 2) show an attempt made just before the war by the present author along the lines we have dwelt upon. Those who are aware of the close attention given *inter alia* to the dispersal of spawning products in many sea areas of the world may be moved by these to give the writer's suggestions a trial.

Before leaving this topic, it might be added that the writer, before embarking on the barometric pressure gradient work, had suggested that oceanographers ought to possess a totalizing anemometer of robust and simple nature. With such, the interconnection of air and water movements could be investigated very far and very easily. It may still be a good idea, but the matter has been left in abeyance for the time being in favour of the present interest.

Note on Wind Presentations. Available were: a large table of wind vectors, one of wind components, and a large sheet of wind anomaly arrows. All the underlying computational work, and the text, were the work of Günter Dietrich working in Hamburg. Fig. 3 is a specimen portion of the half-century long sheet of wind anomaly arrows.

For much assistance in the provision of the requisite barometric data from the British side, acknowledgment is made to the British Meteorological Office. Through the good offices of J. M. Stagg, Branch M.O. 3a of that Office prepared a valuable table of mean values appropriately corrected and adjusted. Thanks are tendered to the head of that Branch and to J. Glasspoole who was involved in the work.

At the time of writing the above essay, the Dietrich wind data had been delivered for only the northern North Sea, although preparation of comparable material for the southern North Sea, for the central North Sea, for Shetland waters, for the English Channel, and for the Irish Sea was going on at the time.

Since then, the wind material for the central and the southern reaches of the North Sea has been received, and use (deemed very satisfactory) has been made of it in connection with the herring, the plaice, and the cod. Some relating remarks are made in the concluding Addendum Note.

ADDENDUM

Note on the Temporal Variations of Wind Conditions Over the Northern North Sea
(Due to Günter Dietrich)

Owing to the important part played by the wind in the water movements and in the oceanographic structure of the sea, wind conditions over the sea are of special interest. It is comparatively easy to obtain wind data above the sea surface either by direct observation or by derivation from pressure distribution. However, only a few systematic series of observations regarding the dependent processes in the sea are available.

Therefore, if it is desired to investigate those processes in certain sea areas, it will be possible to do so only by drawing conclusions for the known wind conditions. So far as the inter-relations between the wind and the processes under study in the sea are established, this offers many advantages over the direct method and is no makeshift.

It is believed that the wind presentations provide the data needed for the application of such a method of investigation of conditions in the northern North Sea. They show the monthly and annual mean wind values for the first half of this century, and they provide a present basis for discussion without considering, at this moment, further inter-relations of the seasonal and secular variations of the wind.

Earlier wind observations were based on personal estimations of the direction and force of the wind and are not free from subjective errors of estimation. Besides, long-period series of wind observations are available for land stations only. Owing to the great differences observed between the conditions of friction above solid ground and those occurring over the sea, land wind data cannot be taken as satisfactory for conditions obtaining over the sea. Further, air currents are locally influenced by the conditions of the ground. For these reasons, it is inadvisable to consider wind observations made at land stations as truly representative of conditions prevailing over greater sea areas.

The summarizing representation of wind conditions (shown in part in Fig. 3) above the northern North Sea (1900 to 1949) has been based on such atmospheric pressure gradients as could be calculated from the corners of a triangle by means of analytic geometry once the atmospheric pressure values were known. The monthly mean values of the air pressure of the Shetland Islands (Lerwick), North England (Tynemouth or Scarborough) and South Norway (Mandal or Oksöy) have been taken as a basis after they had been uniformly reduced to mean sea level and normal gravity at 45° latitude. The centre of this triangle is in the northern North Sea at Lat. 58° N, Long. 2° E. The

underlying air pressure values have been given in various meteorological publications[5] The monthly means of recent years were made available by J. N. Carruthers (Admiralty, London) and by Th. Hesselberg.

It is a well known fact also that air currents above the sea do not correspond to the pure geostrophic winds. Hesselberg and Sverdrup[6] treated the influence of friction exercised by the solid soil, and Baur and Philipps[7] extended the investigations to the open sea. From their results it follows that, on the average, at Lat. 58° N, the wind direction does not turn at an angle of 90° to the right of the direction of the pressure gradient as would happen with no friction existing, but at an angle of 76°; it follows too that the velocity of the surface wind amounts to only 69% of that of the geostrophic wind. An atmospheric pressure gradient of 1 mb/100 Km at Lat. 58° N, with a mean air density of 1.28 KG/m^3, corresponds to a surface wind of 4.35 m/sec. In consideration of these influences of friction, the monthly mean values of the wind above the northern North Sea for the period 1900 to 1949 were derived from the calculated monthly mean values of the air pressure gradient. Data for half a century in tabular form, supplied to J. N. Carruthers but not reproduced here, show monthly mean values of the direction from which the wind blew as well as the appropriate speed in m/sec for each month; also given are the annual mean values and grand mean values of the speed for 1901–1930.

Fig. 3 (data in part only) shows the anomalies of each calendar month referred to the normal mean values of the wind (to 1930) in a way which accentuates far more clearly the peculiarity of each individual month than would be possible by a representation of the mean values of the wind. The arrows for the individual months and years represent the wind which would have to be algebraically added to the normal wind of the monthly mean values (1901 to 1930) to produce the actual conditions; from their length, the speed anomaly of the wind is to be seen immediately. By vectorially adding the individual wind anomalies to the normal wind, it would be possible to arrive at the monthly mean winds set out in the data supplied to J. N. Car-

[5] Monthly Weather Report of the Meteorological Office, London; Meteorological Record of the R. Meteorological Society, London; Journal of the Scottish Meteorological Society, Edinburgh and London. Annual of the Norwegian Meteorological Institute.

[6] Hesselberg, Th. and H. U. Sverdrup. Die Reibung in der Atmosphäre. Veröff. geophys. Inst. Univ. Leipzig., (2) *1* (10), 1914.

[7] *Baur, F. and H. Philipps.* Untersuchung der Reibung bei Luftströmungen über dem Meere. Ann. Hydr. Berl., *66*, 1938.

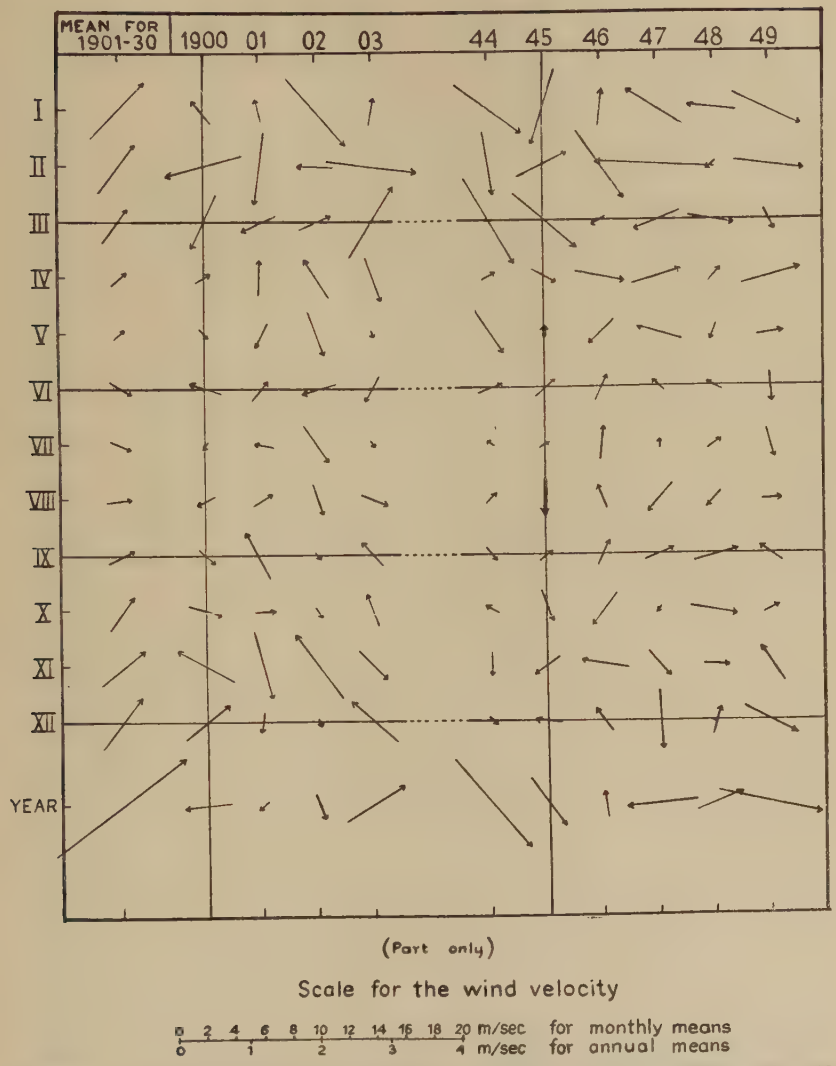

Figure 3. Northern North Sea—Anomalies of the Mean Monthly Winds, 1900–1949, from the Monthly 30-year Means, 1901–1930.

ruthers. It should be observed that the wind speed scale for the annual mean values is five times that used for the monthly means.

Analogous representations for the central and the southern North Sea have also been made available, and further ones for other areas are in preparation.

ADDENDUM NOTE

[Briefly indicating what progress has been made so far along the lines concerned and what is in prospect.]

In the case of the first important food fish to be dealt with, namely the haddock of the northern North Sea, it is expected that a full account of the results obtained will be given in a report to be published from the Aberdeen Marine Laboratory of the Scottish Home Department. Parrish, of that laboratory, who supplied the requisite haddock data and with whom the writer and his associates, A. L. Lawford and V. F. C. Veley, have collaborated closely, gave a brief account of the correlations arrived at when the matter was under discussion in Copenhagen at the time the foregoing essay was tabled and debated. Since then the work has been *polished up* a good deal, but here we shall refer only to its main outcome.

First it must be remarked that Parrish had not been able to explain haddock year-class strength fluctuations either on grounds of temperature or *via* biological reasoning. Using the wind data obtained from Dietrich, work in the oceanographical branch of the Hydrographic Department of the Admiralty led to the discovery (by Veley) of a wind function which successfully accounted for *over 30 years* of fluctuations in year-class strengths of haddock.

There were only two *misfits*, these being for the products from the spawning seasons of 1947 and 1946; of this pair, it seems that the former can be reasonably ascribed to highly unusual temperature (cold) conditions, and the latter to an insufficient area having been covered when the fish census was made *via* trawl hauls. In this connection it is worthy of remark that much brood from the 1946 haddock spawning is known to have been transported to the coastal waters of Norway, a rare event doubtless due to the high prevalence of west wind during the period under consideration.

What emerged from the work was the discovery that wind-caused dispersal of haddock spawning products in one direction was favourable to brood survival; with dispersal in the opposite direction the augury was good also but to a lesser degree; dispersal in *cross directions* was unfavourable in point of survival prospects. These discoveries can be quite well understood on ecological grounds, as will doubtless be shown by Parrish in his future paper.

The outcome in the case of the haddock has fully justified the hope of being able to predict stock recruitment from year to year reasonably satisfactorily in the future, to claim no more.

In the case of herring of the southern North Sea with their main spawning locus in the Cap d'Antifer region off the French Coast at the eastern end of the English Channel, attention was paid to the months

of December, January, and February. The work in this case was carried out by Veley, and, from his preliminary attempts to correlate the fish and wind factors, it appears that the height of spawning probably varies somewhat in time from year to year. In the outcome Veley discovered how to choose the month in which the south-wind factor would be expected to be most important in urging the greatest quantity of herring fry away from land into midchannel. To devote attention thereafter to west wind during the ensuing period, was, he argued, to consider whether the fry would or would not be carried through Dover Straits into the North Sea (a transport held to be beneficial).

The choice of the month within which north-moving wind had to be considered was the crux of the situation, since no approach to predicting power was possible unless the choice could be made. Veley found that the amount of west wind in December was the key to the situation; from that factor he was able to infer the peak month of spawning and thereby learn to which period the south wind factor had to be applied in a given year. In the final outcome, the agreement between wind factors and year-class strengths was established for *upwards of 20* years without *misfits*. Thus good reason now exists for hoping that it may be possible in the future to predict herring year-class strengths satisfactorily from the wind argument by using the procedure formulated by Veley.

Applying identical procedure to the Belgian spent herring industry, a high degree of correlation has emerged between the fortunes of this fishery and wind conditions.

To turn to the plaice of the North Sea is to direct attention to the fish which has been the subject of most thinking in this matter of fry dispersal and survival. Some years before World War II, Bückmann, working from Heligoland, attempted to correlate wind and year-class strengths in the case of the plaice of the German Bight. Veley has since deduced a relationship between wind components in the North-South direction during November and December and the peak time of the plaice spawning.

Without going into detail here, it can be stated that if, on the above deduction, south and west wind be considered for the months dictated, then a completely acceptable correlation emerges. Unfortunately Veley has been limited so far to numerical expressions of plaice year-class quality over a mere ten years.

An investigation carried out by Lawford on the cod of the North Sea shows a connection between brood survival and resultant wind during the principal spawning months, and holds out the possibility of at least qualitative production.

Recently, Dietrich has been able to supply wind data for the English Channel and the Irish Sea. Using these and in part the theories outlined by Hickling in his Buckland lectures, Veley has explained brood fluctuations in the hake hatched to the south of Ireland over a period of ten years.

ANNUAL VARIATIONS IN CURRENT SPEEDS IN THE GULF STREAM SYSTEM[1]

By
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ABSTRACT

The monthly resultant current speeds in ten segments of the Gulf Stream System are calculated from surface current data published by the U. S. Navy Hydrographic Office. Marked annual variations in the current speeds are found in the Florida Current, in the Caribbean Sea, and in the Trade Wind areas. In other segments of the system the annual variations are not so well defined. The maximum current speeds occur during the summer in the southern segments of the Gulf Stream System and during the winter in the northern segments. The minimum speeds occur during the fall months throughout the system. Annual and semiannual periods are calculated and found to be in fair agreement with the observed annual variations in the Florida Current. In the Trade Wind and Caribbean areas the current speed and wind speed fluctuations are approximately the same. A partial correlation is shown to exist between the annual variations in current speeds in the Florida Current and the annual variations in sea level at Miami and Charleston.

The main current system of the North Atlantic Ocean, the Gulf Stream System, obtains its energy of motion principally from the Northeast Trades and the Westerlies. Since the wind system fluctuates in position and velocity with the different seasons of the year, it is to be expected that the current speeds of the Gulf Stream System would also vary with the seasons. Montgomery (1938) and Iselin (1940), on the bases of both hydrographic station data and tide gauge records, showed that there is such an annual fluctuation in the transport of the Florida and the Gulf Stream currents. The purpose of this paper is to show that the many hundreds of surface current observations on file at the U. S. Navy Hydrographic Office also give a consistent picture of annual variations in the current speeds in certain segments of the Gulf Stream System.

The data have been published in the form of an Atlas by the U. S. Navy Hydrographic Office (1946), in which atlas charts are given showing the monthly resultant current direction and speed for each one degree quadrangle in the North Atlantic plus the number of observations used to obtain each value. The following is quoted from the Atlas:

[1] Contribution No. 557 from the Woods Hole Oceanographic Institution. This paper originated as a technical report to the Oceanographic Division of the Hydrographic Office, U. S. Navy Department under a contract with the Office of Naval Research.

> The information relating to monthly resultant surface currents shown on this chart was compiled from observations made during the month for all years prior to 1935 by the cooperating observers of the Hydrographic Office. Observations were not considered reliable where tidal currents prevailed; where winds, sea or swell of force 6 or above were recorded; where the vessel's draft or trim would cause excessive leeway; or when doubt existed as to the meaning of the entry "Nil" on the current report. All current calculations are based on the MEDIAN POSITION method; namely, each observation is applied at only one point, that point being midway between the beginning and end of the ship's run for which the current observation was made.

Because this median position method frequently integrates the speed of the main current with that of possible countercurrents and eddies, the values given in the accompanying tables and figures are much lower than would be the case if they applied only to the main current (Iselin and Fuglister, 1948).

From the Hydrographic Office charts the annual variation in current speeds has been calculated for ten segments of the Gulf Stream System. The areas studied are shown in Fig. 1.

The segments numbered 1 to 7 cover all but the southeastern part of the North Atlantic Eddy, the segments A, B and C take in three branches of the system. The segments were chosen by locating areas where the largest number of observations were available and where the arrows on the charts pointed in approximately the same direction throughout the year. The most doubtful, in regards to area covered, is Segment B in the Antilles Current. The direction of the current arrows and the speeds for each one degree quadrangle varied more in this segment than in any other. Segment 1 in the Trades and Segment A in the Guiana Current have been treated separately because of the marked difference in direction and speed in the two areas. After much of the analysis had been completed, it was found that more quadrangles could have been added to Segment 5 northeast of Hatteras, thus making it a continuous group without changing the results appreciably. Segment 3 in the Florida Current contains the most observations, Segment 1 in the Trade Wind Area the least. For instance, in the month of March, Segment 3 contains 1,468 observations, Segment 1 only 329.

The average of the resultant drifts for all quadrangles in each of the ten segments for each month are given in Table I and are plotted in Figs. 2 and 3. These data indicate that the time of maximum current speed varies as we move around the system. In the southern portions the maximum occurs in summer; in the northern it occurs in winter. On the other hand, the minimum speeds throughout the system occur during the fall months from September to November.

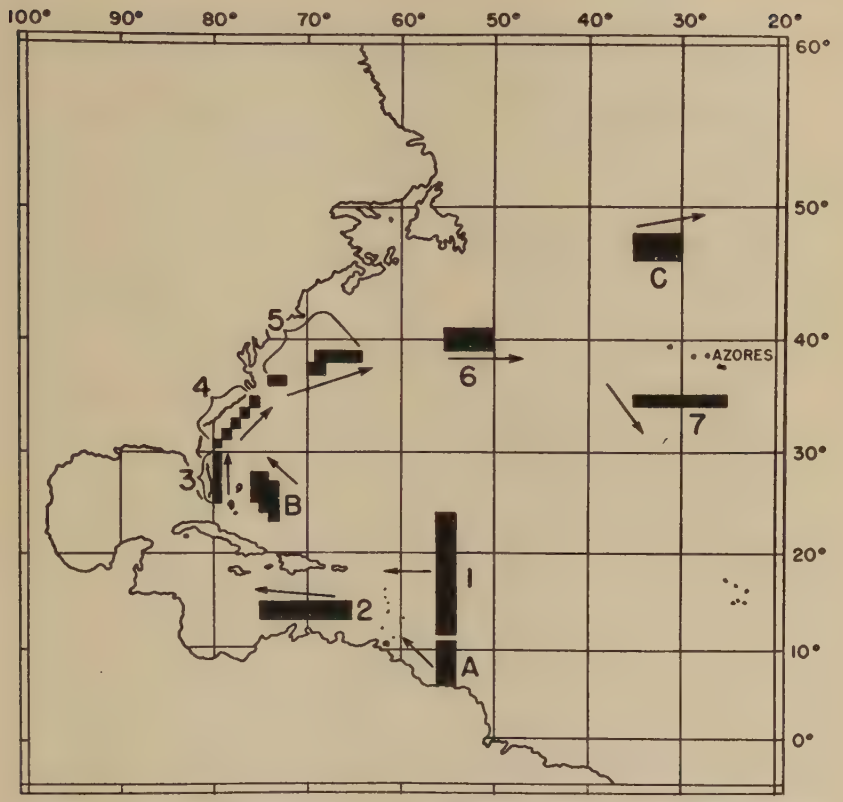

Figure 1. Location of segments of the Gulf Stream System used to calculate annual variations in current speeds. Arrows show resultant current directions within the various segments.

TABLE 1. Average Current Speeds in the Gulf Stream System (Miles Per Day).* See Fig. 1 for Areas Covered by Segments 1 to C.

Month	*Segment*									
	1	*2*	*3*	*4*	*5*	*6*	*7*	*A*	*B*	*C*
Jan.	7.4	17.2	55.2	41.3	23.0	12.4	3.7	24.6	4.7	4.9
Feb.	7.4	17.3	57.5	39.9	22.3	13.0	4.1	25.9	3.9	4.1
Mar.	7.4	17.3	60.8	42.2	21.0	13.5	4.1	23.5	4.6	4.1
Apr.	7.0	17.5	61.7	43.7	24.0	12.6	3.6	29.3	4.9	4.4
May	7.9	16.7	61.7	46.4	24.1	12.9	4.3	34.2	4.0	4.2
June	8.3	18.3	64.2	49.3	23.9	11.6	4.0	24.3	4.6	4.8
July	9.4	19.6	65.6	48.2	22.8	13.1	3.3	18.4	4.8	4.6
Aug.	8.5	18.0	65.4	48.4	22.0	11.7	3.8	17.4	5.0	3.9
Sept.	6.4	15.5	60.5	44.0	21.4	12.3	3.3	15.3	4.3	3.2
Oct.	6.9	13.5	52.4	39.0	20.2	10.5	3.4	15.5	3.5	3.2
Nov.	7.2	12.9	49.0	36.7	20.4	11.1	3.6	19.0	4.6	4.0
Dec.	7.4	15.0	53.8	39.4	20.8	10.7	4.2	19.5	4.5	5.4
Mean	7.6	16.6	59.0	43.2	22.2	12.1	3.8	22.2	4.4	4.2

* Computed from the Hydrographic Office Chart, H. O. Misc. 10,688.

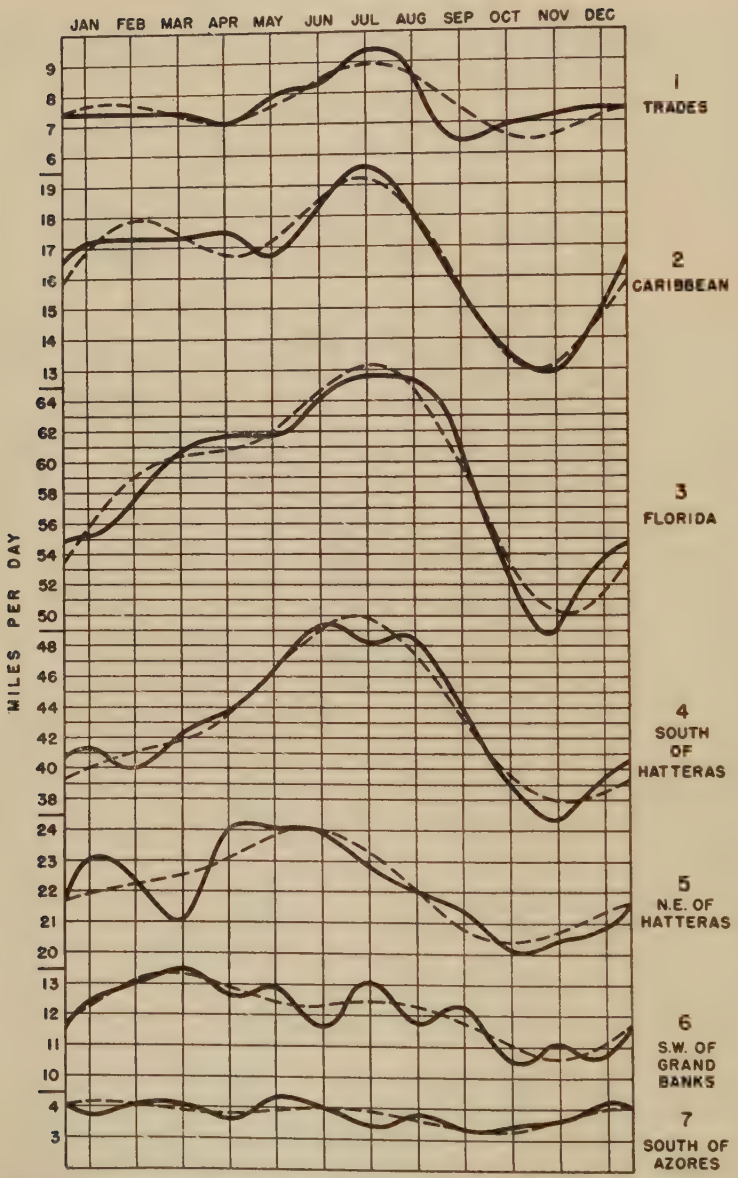

Figure 2. Annual variation in the current speed in seven segments of the Gulf Stream System. Observed data, solid lines; calculated combination of annual and semiannual periods, dashed lines.

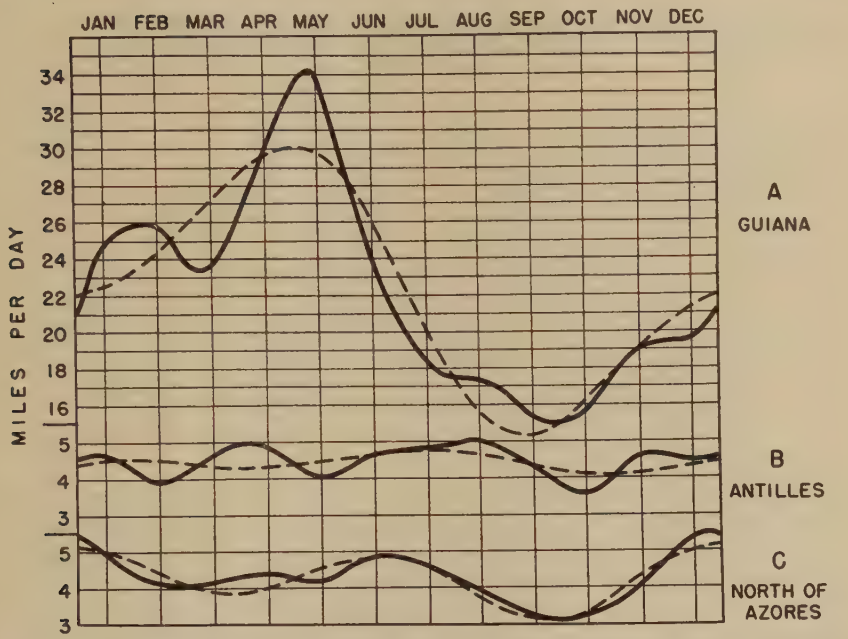

Figure 3. Annual variations in the current speeds of three branches of the Gulf Stream System. Observed data, solid lines; calculated combination of annual and semiannual periods, dashed lines.

In no case does the annual variation curve approximate a simple sine wave. In order to determine how closely a combination of annual and semiannual periods would fit the observed data and in order to determine also the relative importance of these two periods, the values in Table I were analyzed harmonically (Conrad, 1944: 71). The results of these calculations are shown by the dashed lines in Figs. 2 and 3. There is a fair agreement in the calculated and observed annual variations for those segments where the currents are relatively confined, as along the continental shelf south of Cape Hatteras. Because of the meandering nature of the currents in other areas, the actual current speeds and, to a lesser extent, the annual variations are obscured by the averaging processes.

In the southern and eastern segments of the North Atlantic Eddy the amplitudes of the first two harmonic terms, the annual and semiannual periods, are nearly equal. In the Guiana Current and in Segments 3 to 6 in the western and northern part of the eddy the annual period has the greater amplitude. The relative amplitudes, in per cent of the arithmetic mean, for the annual and semiannual periods for each segment are given in Table II.

TABLE II. The Relative Amplitudes of the Annual and Semiannual Periods for Ten Segments of the Gulf Stream System (Per Cent of the Arithmetic Mean)

	Segment									
	1	*2*	*3*	*4*	*5*	*6*	*7*	*A*	*B*	*C*
1st term	8.5	12.4	11.0	12.2	7.0	8.8	7.8	3.1	3.5	9.4
2nd term	8.3	10.6	4.9	4.0	2.6	3.2	6.8	1.0	5.1	16.8

TABLE III. Estimated Wind Speed Component in the Direction of the Current for Eight Segments of the Gulf Stream System (in Meters per Second)

Segment	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*
1	4.7	5.1	4.5	5.3	5.4	6.0	6.5	6.4	5.6	4.4	4.8	5.7
2	6.8	6.4	6.0	6.9	6.6	6.7	7.2	6.0	5.4	4.3	4.7	6.1
3	−1.6	0.0	0.3	−0.2	0.7	1.0	1.5	0.8	−0.4	−0.5	−1.5	−2.3
4	−1.9	−0.1	1.0	−0.1	1.7	2.0	1.4	0.8	−0.6	−2.0	−0.4	−3.5
5	−0.2	0.0	0.2	0.4	−0.3	1.3	2.1	0.4	−0.5	0.3	0.2	0.1
6	2.6	1.6	1.5	1.7	1.2	2.3	3.2	1.9	0.7	1.5	0.5	3.2
7	−0.9	0.4	−1.0	1.1	0.7	1.0	1.0	1.5	0.3	−0.3	1.9	0.2
C	5.2	4.5	3.3	2.0	1.7	1.6	2.1	2.3	2.8	2.3	3.4	5.3

Only in the last two segments, B and C, are the amplitudes of the second term greater than the amplitude of the first. This may have little significance in area B because of the poor correlation of observed and calculated data, but it may be real in area C where the correlation is good. One difficulty concerning Segment C is that it is not certain that it actually is a segment of the Gulf Stream System. The directional arrows on the Hydrographic Office chart for this area are uniform throughout the year, but this is not proof that a northern branch of the System consistently passes through the area. It has been assumed that all the segments dealt with in this study form part of a continuous current system. Whether or not a branch of this system passes through area C, the surface current data from the area include the effects of the shallow wind drift currents. A tabulation of the varying wind velocities for this area (see below) indicates that the annual variations in current speed are due only in part to the wind.

The annual variation in wind force was obtained from the wind roses on the British Admiralty charts of the North Atlantic. These charts show the frequency, force and direction of the wind for each 5° quadrangle for each month. The values shown in Table III are the estimated wind components in the direction of the currents. The values are only approximate owing to the difficulty of reading exact values from the roses and of converting from the Beaufort scale to wind speed. The negative values indicate that the component of the wind force along the streamline of the current is in the opposite direction to its flow.

In only two segments, the Trades (1) and the Caribbean (2), are the wind speed and the current speed fluctuations approximately the same.

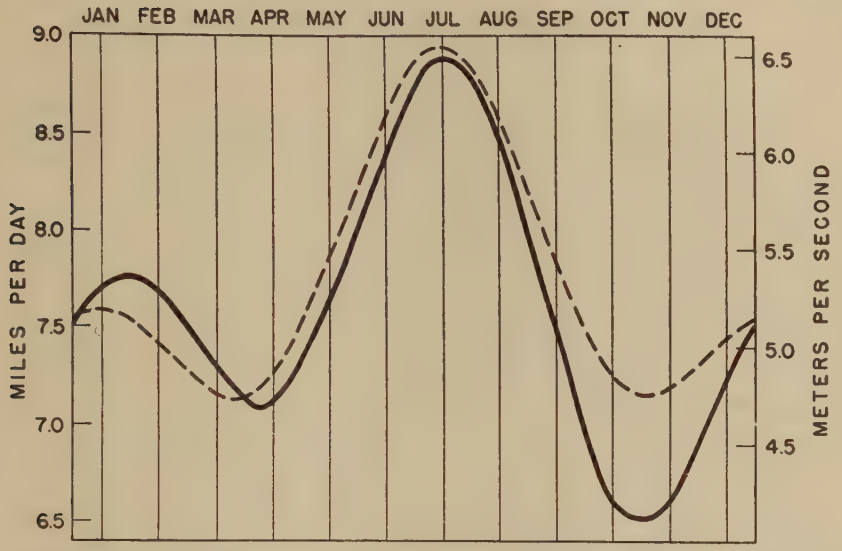

Figure 4. Calculated combination of annual and semiannual periods for the currents, solid line; for the winds, dashed line; segment 1.

This is certainly what should be expected, since these winds are the motive force for the currents. Harmonic analysis of the wind speed data from Segment 1 shows that the resultant of the combined annual and semiannual waves is similar to the resultant for the current speeds (see Fig. 4). The relative amplitudes, in per cent of the arithmetic mean, for the first two terms for the wind data are 12.6 and 9.5 as compared to 8.5 and 8.3 for the current data.

The annual variations in current speed and wind speed for Segments 1, 2 and C are shown in Fig. 5. In Segment C, north of the Azores, it appears evident that the winter maximum in the current speeds must be due in large part to the winds. The secondary maximum in the summer, at a time when the winds are at a minimum, may indicate that this segment is in fact a continuation of the main current system.

Using the method employed by Iselin (1940), the average monthly speeds of Segments 3 and 4 in the Florida Current have been compared with the sea level records from Miami and Charleston. According to this theory the mean sea level is at a maximum when the current speed is at a minimum. The tide gauge records were taken from two papers by Montgomery (1938, 1941). The two sets of curves are shown in Fig. 6. The correlation is only fair; while the winter maximum indicated by the tide gauge records does not appear on the curve of the observed current speeds, both sets of data show the rapid decrease in

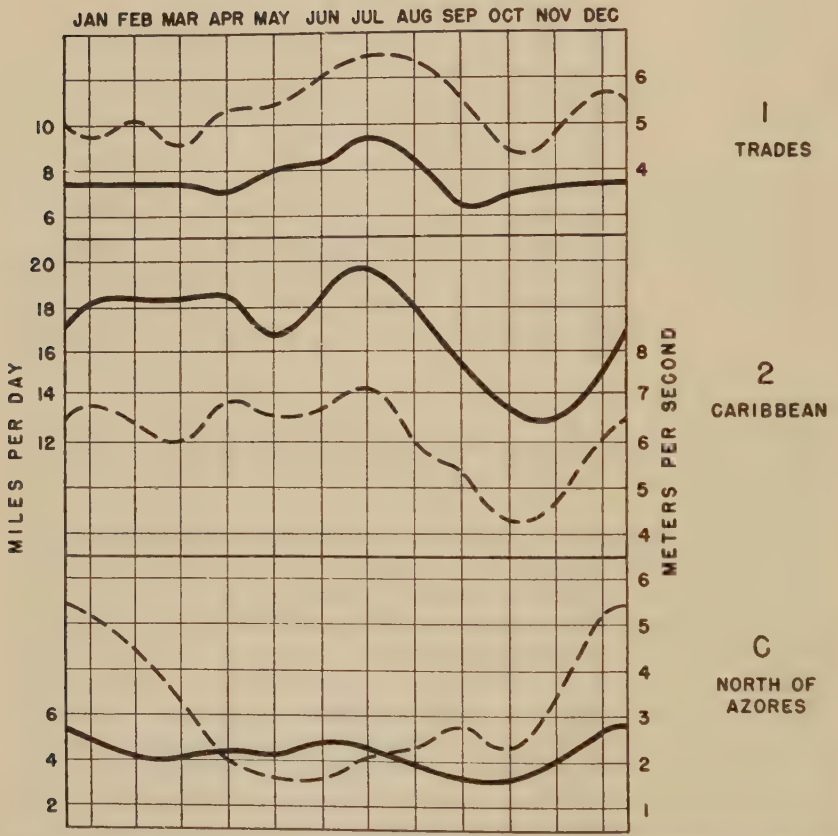

Figure 5. Annual variation in current speed, solid lines; wind components in direction of the currents, dashed lines.

values between July and October. The adverse winds of December and January (see Table III) may account for the absence of a winter maximum in the observed current data.

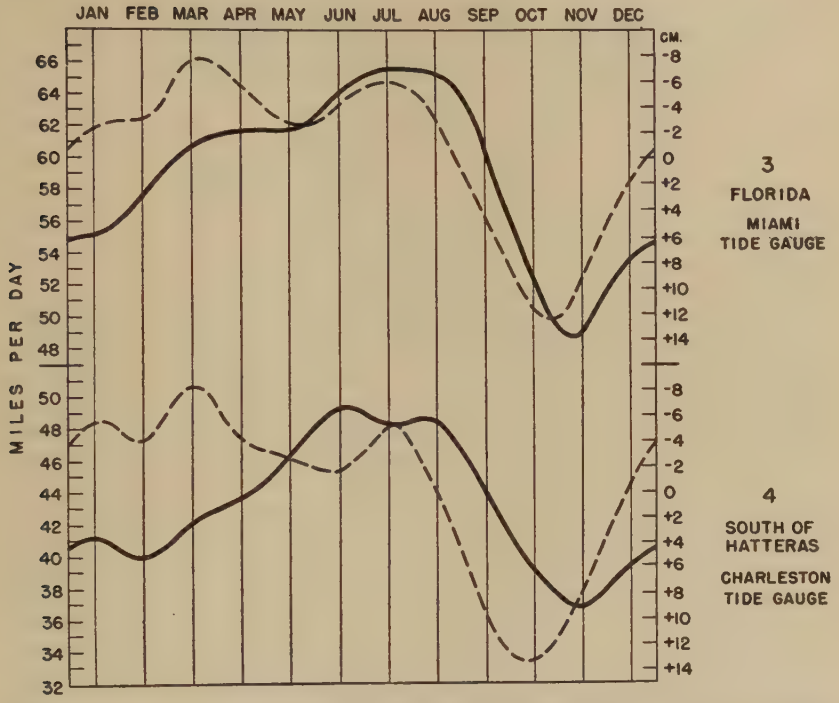
JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC
MILES PER DAY
66 64 62 60 58 56 54 52 50 48
50 48 46 44 42 40 38 36 34 32
CM.
-8 -6 -4 -2 0 +2 +4 +6 +8 +10 +12 +14
-8 -6 -4 -2 0 +2 +4 +6 +8 +10 +12 +14
3
FLORIDA
MIAMI
TIDE GAUGE
4
SOUTH OF
HATTERAS
CHARLESTON
TIDE GAUGE

Figure 6. Comparison of current speeds (solid lines) with tide gauge records (dashed lines).

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THE SOURCES OF THE DEEP WATER OF THE EASTERN MEDITERRANEAN SEA[1]

By

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ABSTRACT

The deep water in the two basins of the eastern Mediterranean Sea, the Levant and the Ionian Sea, is identical in temperature and salinity though differing slightly in oxygen content. Contrary to Nielsen's thesis, none of this water is formed in the southern Aegean Sea. The latter, connected with the Mediterranean by a number of straits, has consistently higher salinities and oxygen values in the vicinity of the sill depths than are found at equal or greater depths on the Mediterranean side of these channels. The effluent from the Strait of Sicily is also eliminated as a source of the deep water since it is separated from the latter by an intervening layer of maximal salinity. The Adriatic Sea has extremely variable water characteristics because of its shallow average depth and consequent susceptibility to fluctuations of the prevailing weather regime. In its southern half, considerable mixing takes place between relatively fresh water from the north and more saline water from the upper few hundred meters of the Ionian Sea. This mixed water sinks and then flows sporadically along the bottom into the Mediterranean Sea, where it circulates counterclockwise. This flow is confirmed by the distribution of oxygen values in the deep layers of the entire eastern Mediterranean.

INTRODUCTION

In his outstanding treatise on the hydrography of the Mediterranean Sea, Nielsen (1912) makes the following statement about the sources of the deep water in the Levantine and Ionian basins:

> We have seen, further, that a uniform layer of water from surface to bottom occurs in the southern part of the Adriatic and in the Aegean Sea north of the Cyclades—possibly also in the deep water north of Crete—and that this layer is colder and heavier than the masses of water, which are found at the same level in the Levant and Ionian Sea. These masses of water will then move towards the south, in the extent to which the depths permit, and after reaching the Ionian Sea and Levant will flow down its northern slopes to the greatest depths. During this movement they will become partially mixed with the bottom-water and be distributed by horizontal currents in the bottom-layer over the whole of the eastern basin.

[1] Contribution No. 556 from the Woods Hole Oceanographic Institution. This investigation was supported by funds under Contract No. N6onr–277 between the Office of Naval Research and the Woods Hole Oceanographic Institution.

Figure 1. Station positions in the eastern Mediterranean Sea.

Schott (1915), in a paper which is largely a review of Nielsen's work, agrees with the above statement but doubts that enough water flows out of the Aegean Sea to fill the Levantine Basin.

The present paper will attempt to show that the deep water is formed only in the Adriatic Sea and that the Aegean Sea cannot contribute to this bottom water mass.

The serial observations of temperature, salinity and oxygen obtained by the Research Vessel ATLANTIS of the Woods Hole Oceanographic Institution during the winter and spring of 1948 form the main source of data for this discussion of the eastern Mediterranean. Earlier stations in the area were also used, with the exception of POLA data which were obtained in the days before the present standards of accuracy were achieved in oceanographic observations. Fig. 1 shows the outlines of the area under discussion and the positions of all stations used.

Vertical convection currents which can cause a complete overturning of the entire water column and can thus be an important factor in the formation of subsurface water characteristics are most likely to occur during periods of minimum surface temperatures. Therefore it becomes important to establish a criterion for comparison of stations taken at different times of the year.

To this end the annual cycle of surface temperatures was plotted for two small areas in the eastern Mediterranean: A one-degree square between Crete and Cyprus, and a two-square-degrees rectangle in the center of the Ionian Sea. Since the data were limited to bathythermograph surface temperatures obtained after 1947, the resulting curves were rather irregular. Nevertheless, the two curves paralleled each

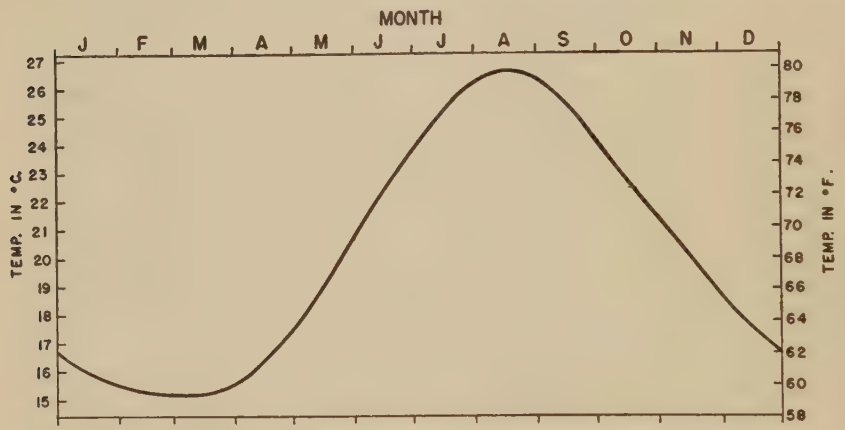

Figure. 2. Mean surface temperature cycle in the eastern Mediterranean Sea.

other closely, the Ionian Sea temperatures being about 1.5° C. colder than corresponding temperatures from the Levantine area. As a check on these data, averaged monthly surface temperatures obtained by British ships between 1900 and 1914 (Meteorological Committee, Air Ministry, London, 1930) were plotted on the same diagrams. Good agreement was found. Since relative rather than absolute temperatures were the feature sought, these different sets of surface data were combined into a mean curve (Fig. 2).

CHARACTERISTICS OF THE DEEP WATER

Before attempting to trace the sources of the deep water of the eastern Mediterranean, it is pertinent to examine its basic characteristics. For this purpose, temperature, salinity and oxygen curves from two centrally located Atlantis stations, 4711 in the Ionian Basin and 4699 in the Levantine Basin, are shown in Fig. 3. On the basis of Fig. 2, both of these stations were made close enough to the period of minimum surface temperatures to be fairly representative of winter conditions except in the upper 50 meters where some warming had already taken place.

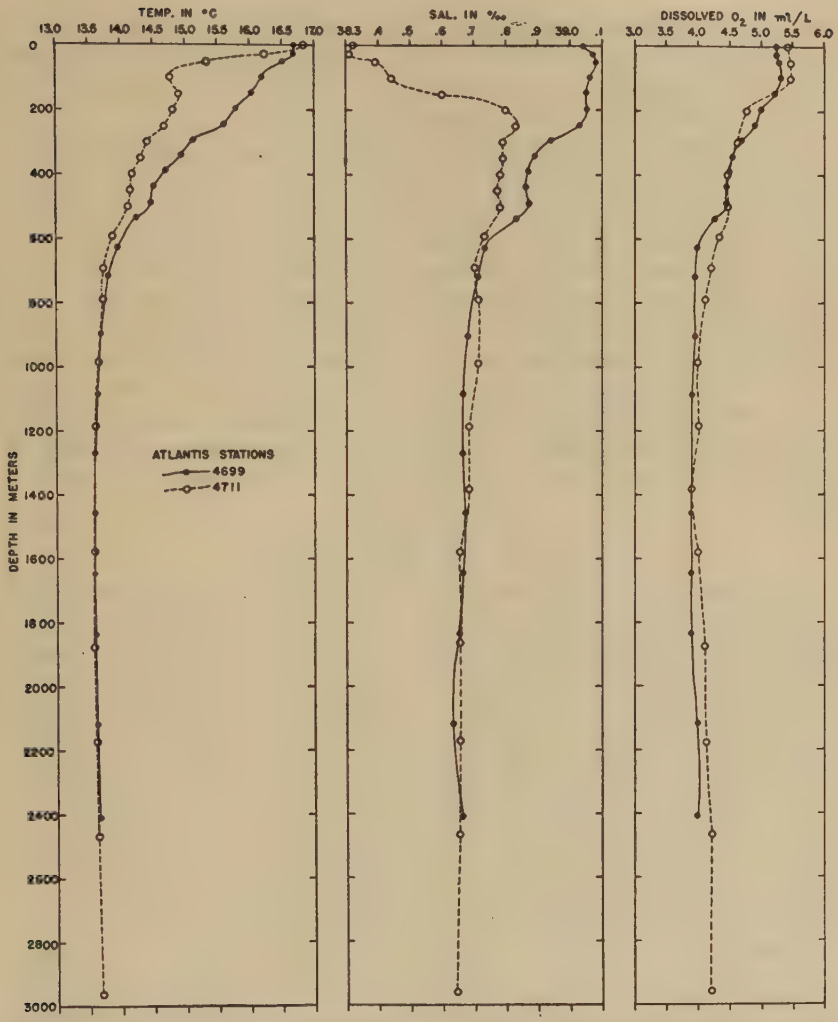

Figure. 3. Typical station curves from the central Levant (No. 4699) and the Ionian Sea (No. 4711).

The significant features of the two sets of curves are their difference in the upper 1000 m or so and their similarity below that depth. The temperature traces practically coincide below 850 m, both having a minimum value of 13.57° C. at 1600 m. The salinity curves show more irregular divergencies. Between 750 m, where the two curves cross, and 1600 m, the traces differ by as much as 0.04 °/₀₀. Below 1600 m,

considering the observational error to be ± 0.02 °/₀₀, both stations are homohaline with a value of 38.65 °/₀₀. The two curves for dissolved oxygen show a striking parallelism below 1000 m, the Ionian station averaging 0.15 ml/L higher than the Levantine one.

If the upper limit of the deep water were defined by marked changes in the gradients of the elements plotted, a depth of about 700 m is the boundary layer. On the other hand, if absolute values are used as the criterion, 1600 m gives a rigorous upper limit for the deep water. For the purposes of this paper, deep water will refer to the layer below 1600 m, with the depth zone from 700 to 1600 m being considered one of transition between intermediate and deep water. These depths are not necessarily representative of the entire eastern Mediterranean; they are merely typical of the water structure in the central section of the two eastern basins. However, they establish a rough criterion for the basic subdivisions of the water column in this area, and, as such, they indicate the magnitude of the thicknesses of the various layers.

THE AEGEAN SEA

As a first step toward analyzing the water movement between the Aegean and Mediterranean seas, a vertical section of temperature, salinity and oxygen through Caso Strait, between the islands of Scarpanto and Crete, was plotted (Fig. 4). Atlantis Stations 4673, 4675 and 4676, used in this plot, were made within a period of four and one-half days, and, according to Fig. 2, they can be considered fairly representative of late winter conditions. Unfortunately, the spacing of these stations, 75 and 92 miles respectively, makes the section far from ideal as far as distribution of data is concerned. In view of their geographical positions, a true bottom profile between them would be meaningless, and hence it was replaced by a schematic bottom curve showing the maximum and minimum depths between stations.

Even considering the subjectivity of the contouring of the station data, several features of the profiles stand out. For all three water properties plotted, the Aegean station (4673) shows weaker gradients and smaller over-all ranges than the Mediterranean station (4676). Station 4675, right over the sill between the two sea basins, shows some characteristics of each of the other two stations. In the upper 400 m, the temperature and salinity structure of this station closely resembles that of Mediterranean water. The oxygen distribution, on the other hand, differs somewhat from that of the other two stations, the gradients being smaller. Below 400 m, the water structure, in terms of all elements considered, is similar to that of Station 4673.

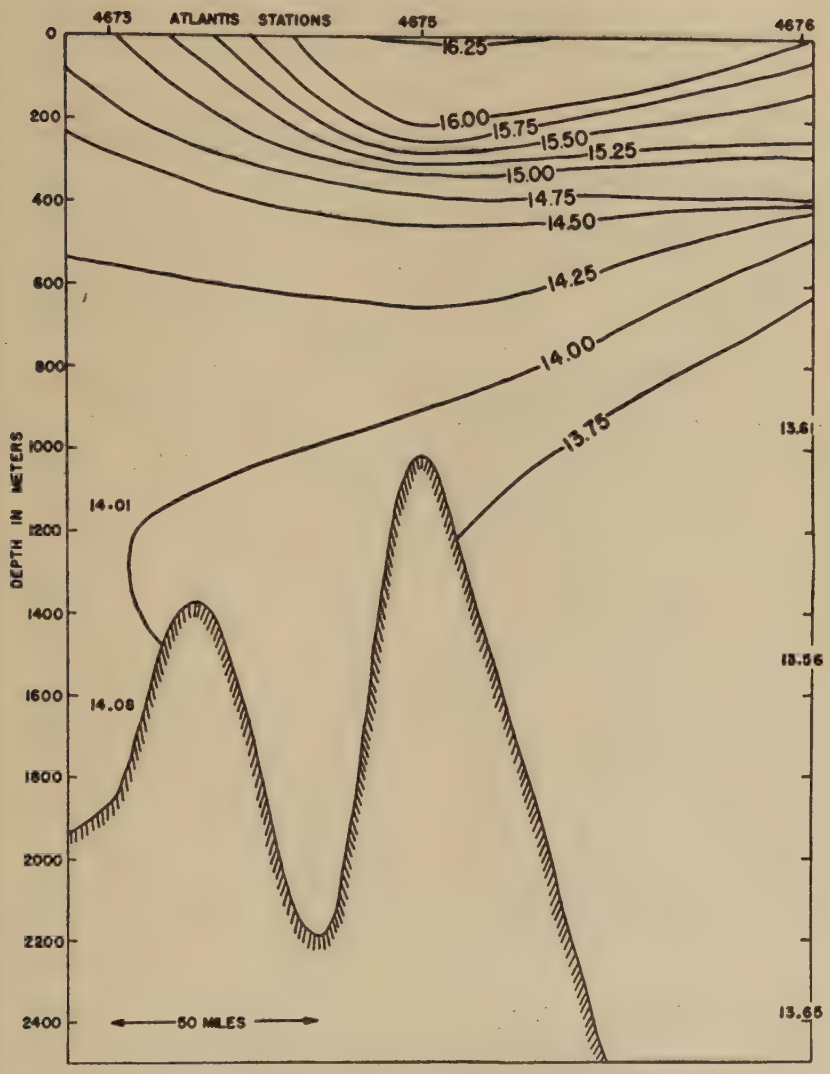

Figure 4a. Temperature section in °C. through Caso Strait.

The surface features indicate a marked flow of Mediterranean water into the southeastern Aegean. This assumption agrees with Nielsen's (1912) analysis of the water movements of the region. The discrepancy between the dissolved oxygen distribution and thermohaline structure at Station 4675, not explainable on the basis of dynamic considerations, is probably due to biological factors.

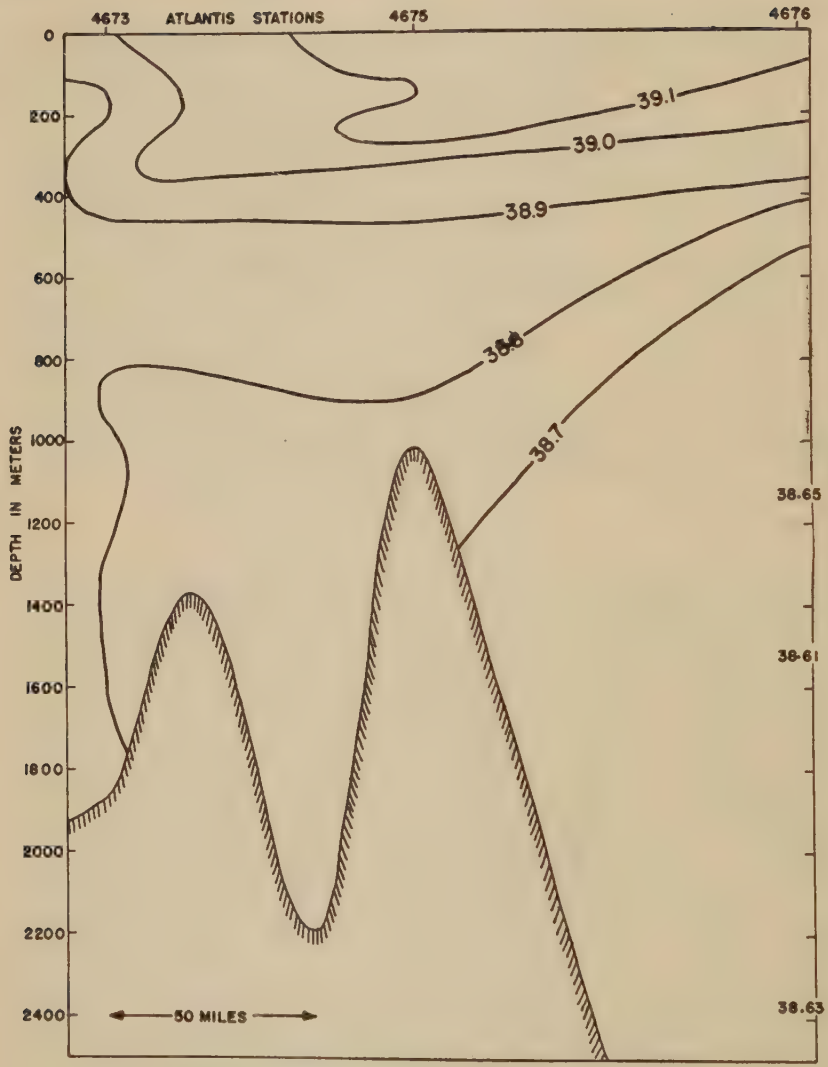

Figure 4b. Salinity section in °/₀₀ through Caso Strait.

Relative to the main question at hand, the significant fact is *not* the inflow of Mediterranean water at the surface but the apparent failure of Aegean water to flow out at the bottom. This situation is indicated by all the isopleths shown in Fig. 4. However, it is brought out most clearly in the section for dissolved oxygen. On Station 4676 there is

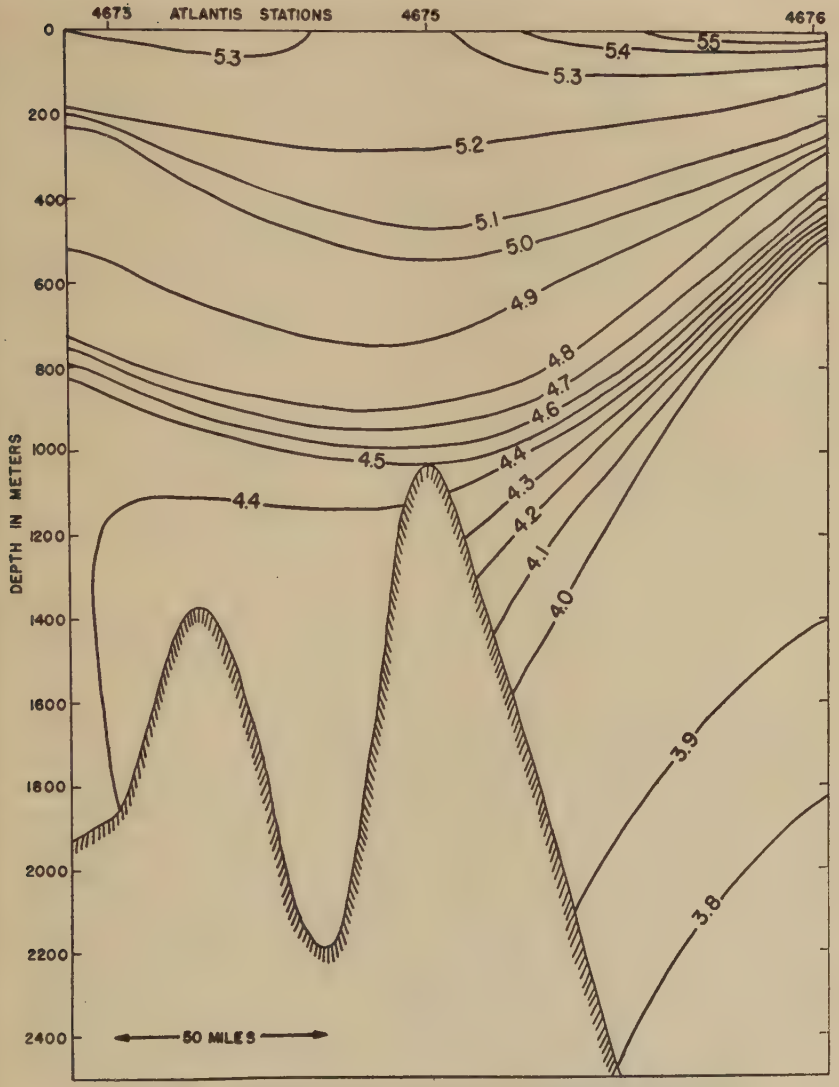

Figure 4c. Dissolved oxygen section in ml/L through Caso Strait.

a sharp gradient at 450 m. Here the oxygen values drop from 4.6 to 4.0 ml/L in 120 m, corresponding closely to the gradient at 550 m found on Station 4699 (Fig. 2). A similar gradient is completely absent on Station 4673, and probably on Station 4675 as well unless an extremely complex configuration of the isopleths is accepted. Since

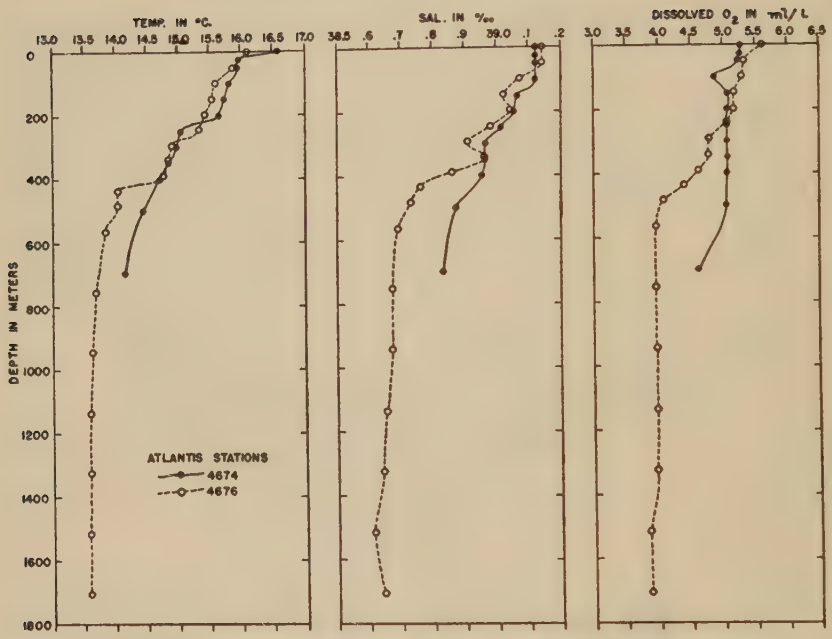

Figure 5. Station curves on either side of the Strait of Scarpanto.

Nielsen's thesis implies a downward and outward flow of Aegean water across the sill, it is very likely, if such a movement were present, that temperature, salinity and oxygen values at Station 4676 would show some increase below the sill depth of 1000 m. There is no evidence of such an increase in any of the elements shown. The increase in temperature below 1500 m is due to adiabatic heating, as pointed out by Nielsen (1912) and confirmed by the present ATLANTIS observations.

Between the islands of Scarpanto and Rhodes lies the second major channel into the southeastern Aegean, the Strait of Scarpanto, with a sill depth of 880 m. While no station was occupied in this Strait, Station 4674 in the Aegean and 4676 in the Mediterranean fall roughly in line with it. Fig. 5 compares the vertical temperature, salinity and dissolved oxygen distribution of the two stations. The temperature and salinity plots show a marked similarity from the surface to about 375 m, thus furnishing further evidence of the surface flow into the Aegean. In this connection it should be remembered that the surface water at Station 4674 may have entered the Aegean through Caso Strait rather than Scarpanto Strait. Unfortunately this problem cannot be resolved by means of the available data. However, the current

pattern in the eastern Mediterranean, plus the width, depth and orientation of the two straits, makes it appear likely that surface water enters the Aegean through both of them.

The two corresponding station curves for dissolved oxygen, by contrast, show marked differences at all depths. In the upper 300 m, where the distribution of temperature and salinity is essentially similar, the Aegean station has lower values. Below this depth, the Mediterranean station has a lower oxygen content. This discrepancy between the different water characteristics resembles that found in the section through Caso Strait (with Station 4674 being similar to 4675 in the Strait rather than to Station 4673 in the Aegean proper).

The third channel into the Aegean between Rhodes and Asia Minor is only 350 m deep. No observations were made close enough to this channel to permit an analysis of its currents. However, *Sailing Directions for the Mediterranean* (U. S. H. O., 1942) indicate that its surface current generally sets to the westward. This is in complete agreement with the general nature of surface currents in this part of the Mediterranean. In view of the depth of surface inflow through Caso and Scarpanto straits (400 and 375 m respectively), it appears equally certain that the sill depth of this channel would prevent any subsurface outflow from the Aegean by this route.

In the southwestern Aegean only one of the three passages into the Mediterranean has an appreciable sill depth. This is Andikithira Channel, north of Crete, with a maximum depth of 805 m. The other two channels have depths of 137 and 290 m. The station in the Aegean Sea closest to these channels is Station 4670, 25 miles due north of Andikithira Channel, while Station 4671 is 41 miles east-northeast of that position.

Station 4670, which was occupied after a day of high winds, showed a thoroughly stirred surface layer 500 m thick. From this depth to the lowest observation at 865 m, small negative gradients were found in temperature, salinity and dissolved oxygen. In the mixed layer the salinity had a value of 38.96 °/₀₀, at 865 m it was 38.86 °/₀₀. Although Station 4671 had a surface salinity of 39.10 °/₀₀, typical of the water entering the Aegean from the northeastern Levant, its salinity at 895 m was only 38.83 °/₀₀. Since depths of 865 and 895 m are well below the sill of the channel, and since their corresponding salinities are about 0.20 °/₀₀ higher than those of the deep water of the eastern Mediterranean, it should be evident that the southern Aegean cannot be a main source of this water. It could be a major source only if its subsurface outflow were mixed with water of considerably lower salinity to give an average of 38.65 °/₀₀.

THE STRAIT OF SICILY

As the evidence presented appears to eliminate the Aegean Sea as a source of the eastern Mediterranean deep water, the only other two possible sources must be examined minutely. These are the western Mediterranean, via the Strait of Sicily, and the Adriatic Sea.

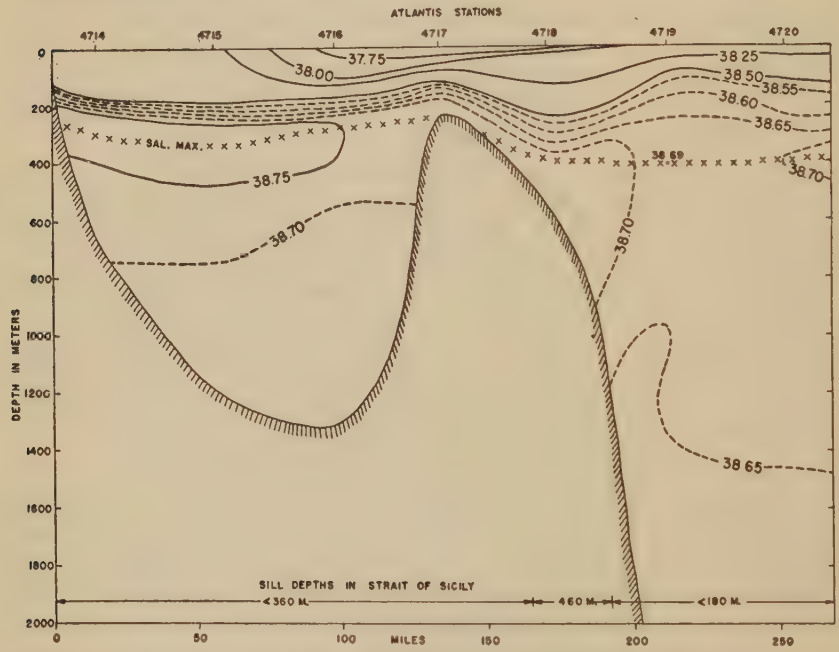

Figure 6. Salinity section in °/oo east of the Strait of Sicily.

The Strait of Messina was ruled out as a major channel for water transport between the western and eastern Mediterranean by Nielsen (1912) on the basis of the tidal nature of the currents. The small net transport through the Strait is confirmed by Vercelli (1925). Since the minimum width of the Strait is only 1.7 miles and the sill depth 110 m, the mass transport through it, even under conditions of unidirectional flow, would be very small compared to that through the Strait of Sicily or the Strait of Otranto.

Fig. 6 shows the salinity profile for a north to south section running from the Gulf of Sidra to the east coast of Sicily. This section was made during the last days of April, and, while not representative of winter conditions, it is sufficiently close to that season to be used in the following analysis.

The station depths vary greatly, since the section was run close to the edge of the shelf which drops off sharply from the eastward extension of the Strait of Sicily to the Ionian Basin. The significant depths in this section, however, are the sill depths of the Strait. These are indicated in Fig. 6.

Figure 7. Maximum salinities in °/₀₀ in the eastern Mediterranean Sea.

The most striking feature of the section is the layer of fresher surface water at Stations 4716, 4717 and 4718. This is the core of the current which enters the Mediterranean through the Strait of Gibraltar as Atlantic water and then follows the African Coast through the Strait of Sicily as far east as the Levantine Coast, where it gradually changes its characteristics. Considering the lower boundary of this current to be represented by the midpoint of the sharpest positive gradient at each station, we find its depths to be 125, 75 and 25 m respectively. To the south and north of this main current, even though the surface salinities are considerably higher, a positive salinity gradient is still present in the upper layer. At Stations 4714 and 4715, to the south, the midpoint of the maximum gradient is found at 175, while at Stations 4719 and 4720, to the north, it is found at 25 m.

Throughout the section a maximum salinity, marked by x, occurs below the positive gradients at depths between 250 and 400 m. These depths are generally close to the sill depths in the eastern extensions

of the Strait. The absolute sill depth of the Strait of Sicily, northwest of Pantelleria, is only about 320 m. This situation leads to the conclusion that the water entering the eastern Mediterranean from the west is limited to the upper few hundred meters and that the most saline water found in this section is formed in the eastern basins.

The maximal values mentioned decrease from 38.79 °/₀₀ in the south to 38.69 °/₀₀ in the north. Even this lowest value is still 0.04 °/₀₀ higher than that found in the deep water. Hence, the layer of maximum salinity can contribute to the formation of deep water only by mixing with a water mass of salinity less than 38.65 °/₀₀. In the present section such water is found only in the surface layer. But if the mixing and sinking required to produce the bottom water were taking place in this region, a vertical zone of isohaline water of salinity about 38.65 °/₀₀ would have to appear. Such is not the case.

In order to determine whether such a process involving the surface layer is going on to the eastward of the above section, it is merely necessary to plot the maximum salinities for all available winter stations. This is done in Fig. 7, which shows that maximal salinities increase to the eastward, forming an increasingly impenetrable horizontal barrier between surface and deep water.

THE ADRIATIC SEA

We now come to the last possible source of the deep water, the Adriatic Sea and northern Ionian Sea. These two basins are connected by the 40-mile-wide Strait of Otranto, with a sill depth of 780 m.

Station data from the Adriatic are relatively plentiful. Between the years 1911 and 1914 the ships NAJADE and CICLOPE made a series of comprehensive cruises, reoccupying the same stations a number of times at different seasons. Since the sections run by the two ships overlap to a considerable extent, and since the CICLOPE stations are incomplete in their subsurface sampling, the following remarks concerning the Adriatic are based on NAJADE data alone. It is felt that these furnish adequate geographical and seasonal coverage for the purpose at hand.

An examination of these data shows a considerable variation from year to year for the same season. For example, in February 1912 the maximum surface salinity was found to be 38.53 °/₀₀ at a position in the Strait of Otranto, while in March 1913 the maximum value was 38.81 °/₀₀ at a position about 150 miles northwest of the Strait. These marked changes are not surprising when it is considered that only one-quarter of the Adriatic Sea extends to depths greater than 200 m, with an average depth for the entire Sea in the neighborhood of 300 m.

This, of course, implies that a major portion of Adriatic water is directly affected by the prevailing weather regime. It is of interest to note that during the 1912 cruise, when surface salinities were low, the wind was blowing from directions between NE and NW 22% of the time and from directions between S and SE 21% of the time. Cor-

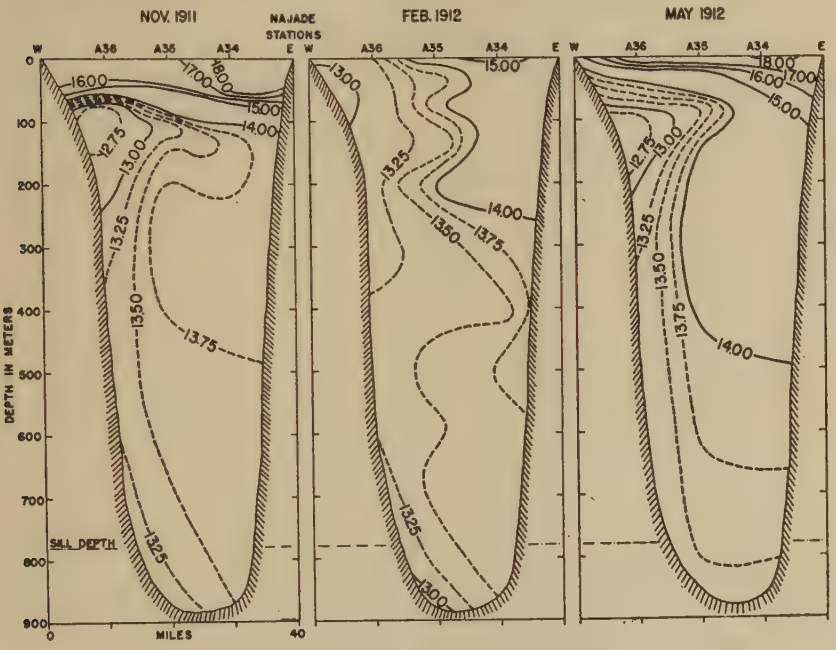

Figure 8a. Temperature sections in °C. across the Strait of Otranto.

responding figures during the 1913 cruise of high surface salinities were 11% from the north and 41% from the south. This suggests that the amount of Mediterranean surface water entering the Adriatic will fluctuate with the frequency of southerly and southeasterly winds over the area.

Fig. 8 shows three sections made in successive seasons across the Strait of Otranto. No summer section was made in this vicinity. In examining these profiles it should be kept in mind that the vertical scale is exaggerated by a factor of 185. According to both Nielsen (1912) and Feruglio (1912) who made independent studies, using different data, there is a counterclockwise circulation of the surface water in the Adriatic. This is comparable to the circulation in the Mediterranean proper as well as to that in the Aegean. The existence of this current, which enters and leaves the Adriatic through the Strait

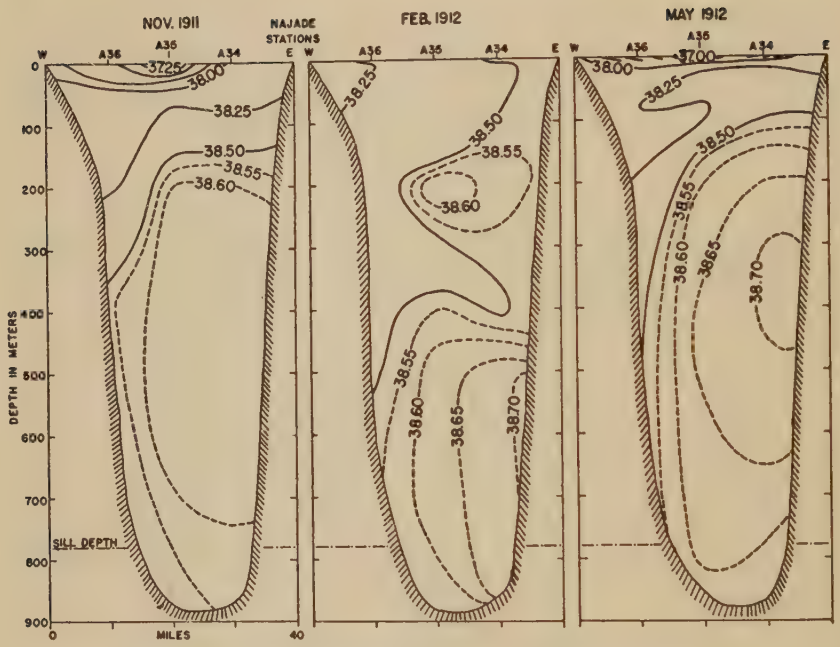

Figure 8b. Salinity sections in °/₀₀ across the Strait of Otranto.

of Otranto, much less its lower boundary, cannot be determined from the sections shown. This is largely the result of the rather small temperature and salinity gradients found below 25 m. While the current may well be limited to such shallow depths, there is no clear cut evidence for or against this assumption.

Despite the variations in the subsurface water structure found from section to section, one feature is common to all of them. All isopleths have a definite vertical tendency resulting in an appreciable variation of all elements from east to west across the Strait.

Temperature and salinity tend to decrease toward the west while dissolved oxygen content shows a slight and poorly defined increase in the same direction. The temperature and salinity values found below 200 m in these sections straddle the values representing typical Ionian Sea deep water (Fig. 3). Only the oxygen values are consistently higher. Although dissolved oxygen, even below the photic zone, is a much cruder indicator of water movement than salinity or temperature, being subject to consumption by varying quantities of plankton, its distribution can shed light on dynamic processes if used with caution and in conjunction with other indicators.

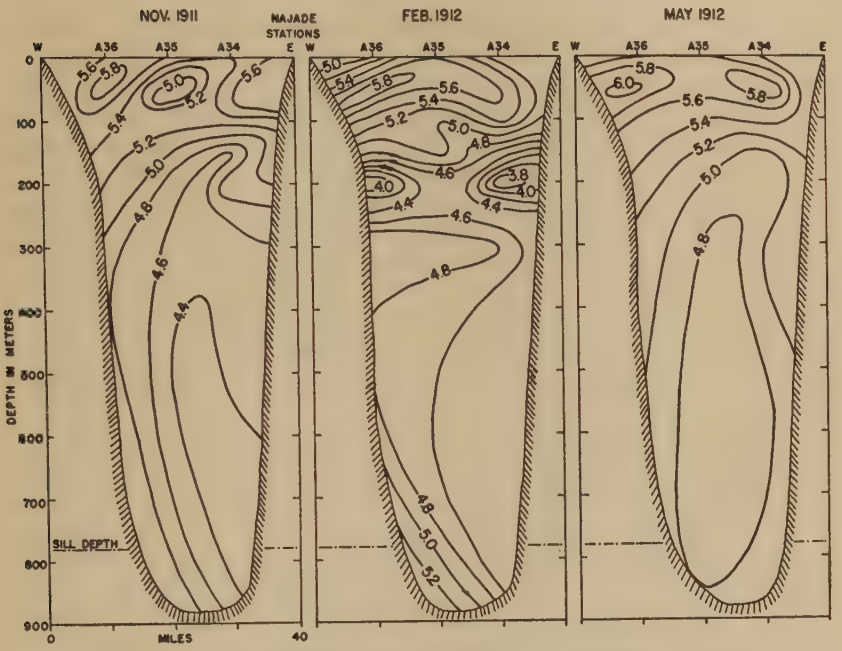

Figure 8c. Dissolved oxygen sections in ml/L across the Strait of Otranto.

In the present sections, it should first be pointed out that the two low O_2 values at 200 m in February 1912 are subject to doubt. While nothing in the original data indicates any lower accuracy for these two values than for others obtained, the two are so inconsistent with the remainder of the data that their validity must be questioned. This, however, is only of minor importance to the problem at hand. If the O_2 values in the deeper water were similar, or even lower, than those of the central and eastern Ionian Sea, then there would be considerable doubt about the direction of flow through the Strait of Otranto.

Since the amount of dissolved oxygen below the zone of photic activity and aeration by mixing can never increase—in fact, will generally diminish due to utilization by plankton or decomposing organic material—there exists a rough inverse correlation between the dissolved oxygen content and the time elapsed since the formation of the particular water mass. If subsurface water flows out of the Adriatic Sea, we should expect its dissolved oxygen content to decrease with increasing distance from the Strait of Otranto.

Fig. 9a shows isopleths of dissolved oxygen for the minimum value throughout the eastern Mediterranean. Only those station data were

used where higher values were found below the minimum. Fig. 9b gives the maximum O_2 values below the minimum. In addition to Atlantis stations, those made by Thor and Dana were also used. The existence of an oxygen minimum at mid-depths indicates that the deep water enters the Ionian Basin near the bottom rather than at mid-depths, gradually rising to the depth of the O_2 minimum layer as it is replaced by newer water at the bottom. While the oxygen minimum layer is therefore not in the direct line of flow out of the Adriatic, it seems reasonable to assume that its values will reflect the maximum values in the water below it. These maximal values, however, cannot be determined with the same degree of certainty as the minimal ones because of the failure of many stations to reach the sea floor, and because of the limiting presence of the irregular bottom itself.

Despite the difference in reliability and significance of the two figures, it is worth noting that some of their general features are strikingly similar. In both cases the highest O_2 values, next to those in the Strait of Otranto, are found along the western side of the Ionian Sea below the sill of the Strait of Sicily and Malta Channel. Here the oxygen isopleths follow the edge of the shelf rather closely, both showing an eastward bulge near latitude 35° N where the bottom contours show a similar configuration. Though differing in detail, both charts have the lowest O_2 values in a tongue of water extending from the eastern end of the Levantine Basin through the eastern Ionian Sea almost to the Strait of Otranto.

The pattern of O_2 distribution leads to the conclusion that subsurface water flows out of the Adriatic, sinks well below the sill depth of the Strait of Sicily and follows the western and then the southern side of the Ionian Sea in a slow drift along the bottom. Since the Coriolis' force tends to deflect the water to the right, it continues along the African Coast into the Levantine Basin rather than forming a closed circuit in the Ionian Sea. This confirms Nielsen's (1912) thesis on the circulation in the deep water of the Ionian Sea. The eastern and northern sectors of this circulation are not clearly defined. This is not surprising when it is considered that the water flowing out of the Adriatic mixes continuously with the water in the eastern Mediterranean, thus gradually losing its characteristic oxygen distribution. Furthermore, on the basis of the changeable water structure in the Adriatic, it is probable that the outflow from that Sea has varying characteristics which are reflected in the irregularities of a composite diagram, such as Fig. 9, where station data from different years and seasons are used synoptically. Another probable source of irregularities in the oxygen data is the indeterminable effect of biological activity on oxygen consumption.

Figure 9a. Minimum dissolved oxygen in ml/L in the eastern Mediterranean Sea.

Figure 9b. Deep maximum dissolved oxygen in ml/L in the eastern Mediterranean Sea.

TABLE I. Potential Density at the O_2 Maximum Below the O_2 Minimum in the Eastern Mediterranean (T, Thor; D, Dana; others, Atlantis)

Station	σ_θ	*Station*	σ_θ
T189	29.21	4707	29.16
4720	29.17	4706	29.18
4644	29.17	4704	29.19
4719	29.18	4701	29.18
T143	29.15	4700	29.16
4716	29.18	T156	29.19
4715	29.19	T160	29.18
T15	29.15	4699	29.16
D4076	29.22	4679	29.16
D4064	29.17	4680	29.13
4711	29.19	4682	29.15
T144	29.19	4683	29.16
4712	29.20	4696	29.16
T145	29.17	4689	29.16
T147	29.17	4690	29.17
D4075	29.20	4693	29.15
4709	29.18	4691	29.18
4646	29.13		
4708	29.17	Mean 29.173	
D4070	29.17	Range 29.13–29.22	
T152	29.18	Standard deviation = 0.019	
D4067	29.18	Mean deviation = 0.015	

TABLE II. Potential Density in the Strait of Otranto Above and Below the Sill Depth of 780 Meters

Najade	*November 1911*		*February 1912*		*May 1912*	
Stations	*Depth* (*m*)	σ_θ	*Depth* (*m*)	σ_θ	*Depth* (*m*)	σ_θ
A36	370	29.11	570	29.13	390	29.06
A35	600	29.11	700	29.12	600	29.07
	860	29.15	800	29.13	800	29.14
			878	29.16	850	29.13
A34	600	29.09	600	29.13	600	29.08
	850	29.10	800	29.16	800	29.10
			855	29.17	860	29.11

In order to test the theory that the Adriatic outflow hugs the bottom as it enters the western Ionian Sea and rises to mid-depths only gradually as it is replaced by newer Adriatic water, a comparison was made of potential densities in the southern Adriatic and in the deepest layers of the Ionian and Levantine basins. Table I lists σ_θ values at the deep O_2 maximum for the entire eastern Mediterranean. Table II

TABLE III. Potential Density between 500 and 800 m at Najade Station A28. Position within 4 Miles of 41° 16′ N, 18° 15′ E

	Depth		
Date	*800 m*	*600 m*	*500 m*
3 Mar. 1911	29.20	29.20	29.18
26 May 1911	29.22	29.15	29.16
24 Aug. 1911	—	—	29.13
29 Nov. 1911	29.27	—	29.20
26 Feb. 1912	29.18	29.17	29.15
28 May 1912	29.28	29.18	29.18
24 Aug. 1912	29.16	29.16	29.14
26 Mar. 1913	29.19	29.16	29.13
23 May 1913	29.16	29.13	29.13
24 Aug. 1913	29.20	—	29.13
23 Nov. 1913	29.21	—	29.12
1 Mar. 1914	29.14	29.14	29.12
Mean	29.20	29.16	29.15

lists the σ_θ values for the three sets of Najade stations in the Strait of Otranto shown in Fig. 8. For the westernmost station, A36, only the deepest observation is given, while for the other two stations σ_θ is given for observations above and below the sill depth of 780 m.

An inspection of the two tables reveals a substantially higher potential density in the deep Mediterranean water than in the observations around the sill of the Strait of Otranto. This is in direct contradiction to the conditions necessary to fulfill the requirements of the postulated theory. Unless the Adriatic water is of equal or higher potential density it will not flow downslope into the depths of the Ionian Sea. However, it should be remembered that the Najade observations were made in different years than the Thor, Dana, and Atlantis observations with which they were compared.

The key to this puzzling situation is found in Najade Station A28, which was occupied on every one of that vessel's 12 cruises in the Adriatic. This station is located 60 miles north of the Strait of Otranto and somewhat closer to the southwestern than the northeastern shore of the Adriatic. With a counterclockwise circulation in that Sea, it can reasonably be assumed that the station is located outside the northward flowing water. Table III gives the potential density at a depth 20 m below the sill and at two depths well above the sill. It is evident from these figures that during a majority of the time there will exist at least a shallow layer of water at the bottom of the Adriatic which has a sufficiently high density to sink to those depths of the eastern Mediterranean at which the deep oxygen maxi-

mum was found. Since the rapidity with which the fluctuations of temperature and salinity in the Adriatic take place is not known, there is no way of evaluating the significance of the sampling portrayed by the values in Table III. However, there is little reason to doubt that the deep outflow through the Strait of Otranto is far from continuous.

A more detailed examination of Station A28 made on 3 March 1911 discloses that the entire water column appears to have been recently mixed. Potential temperatures vary between 12.78° and 13.12° C. and salinities between 38.57 and 38.64 °/₀₀. Salinities at 500, 600 and 800 m were 38.62 and 38.64 °/₀₀, while all values above these depths as well as the value at 1000 m, near the bottom, were either 38.57 or 38.58 °/₀₀. All potential densities fell in the range from 29.18 to 29.22 g/L. The dissolved oxygen values furnish the clearest indication of recent and complete mixing. They vary between 5.7 and 5.9 ml/L, giving a minimum concentration of 97% of saturation value.

Among all the NAJADE and CICLOPE data from the Adriatic, the above station is the only one displaying this degree of homogeneity. Among some of the other deep stations part of the water column was well mixed but never the entire column from surface to bottom. The fact that this situation occurs only once in the data at hand merely proves that the condition is possible; it sheds no light on the frequency of occurrence. Nevertheless, it tends to substantiate the irregularity of the water structure in the Adriatic, and, concomitantly, that of the outflow near the bottom.

Since the Adriatic water which flows out of the Strait of Otranto near the bottom is a mixture of water masses having higher and lower salinities than that of the end product, it seems appropriate to identify the sources of these component masses. Low salinity water enters the Adriatic in the form of surface inflow from the Ionian Sea (as seen in Fig. 8) and as fresh water, the latter largely from the rivers of northern Italy. Since there is no evidence of excess evaporation from the Adriatic, such as is clearly indicated in the Levant by the high surface salinities, the only way in which the total salt content of this Sea can be maintained is through an influx of water of higher salinity than that of the outflowing deep water. The only possible sources of such water are the surface and intermediate layers in the northeastern Ionian Sea. Fig. 8 exemplifies the situation where the surface inflow is relatively fresh while the saltier water is found from 150 m all the way to the bottom on the eastern side of the Strait of Otranto.

However, as was pointed out previously, the surface salinity in the Adriatic varies greatly from year to year. For instance, during the seven NAJADE cruises between February 1911 and September 1912, the maximum surface salinity fluctuated between 38.34 and 38.58 °/₀₀,

whereas during her five subsequent cruises between March 1913 and February 1914 it lay in the range from 38.69 to 38.81 °/₀₀. Where high surface salinities appear in the Adriatic, vertical salinity gradients become small and the boundary between surface and intermediate water becomes less distinct.

The water structure at Station A28 of 3 March 1911 strongly suggests the mechanism whereby the deep water of the eastern Mediterranean is formed. Surface and intermediate water of Mediterranean origin, down to a depth of several hundred meters, flows into the Adriatic, is thoroughly mixed there with fresher water by the vertical convection set up by surface cooling in winter, and then flows back into the Ionian Sea along the western side and bottom of the Strait of Otranto.

As the high salinity surface water flows in from the south, its temperature is somewhat higher than that of water formed in the Adriatic. Consequently, its density will be lower than that of intermediate water with approximately the same salinity. The resulting stability of the water column probably accounts for the infrequent occurrence of such thoroughly mixed water as was found on the above station. In other words, stability of the upper water column is generally maintained either through the low salinity of Adriatic water or through the high temperature of Ionian Sea surface water.

The Adriatic bottom water which flows south into the eastern Mediterranean is probably formed by the gradual sinking of water from mid-depths of the Adriatic. This water, in turn, may be replaced by water drawn in horizontally from contiguous areas or by water sinking from the surface layer above it when the stability of the column is slight, as on the above mentioned Station A28, or by a combination of horizontal and vertical advection. It is significant, for instance, that in the three sections across the Strait of Otranto, shown in Fig. 8, the dissolved oxygen percentage of saturation below 300 m in the western half of the channel averages roughly 82%. If the outflowing water were drawn largely from the surface layer in the Adriatic, this percentage would be much closer to the saturation value, considering the short distance from its source.

As the average oxygen saturation percentage in the eastern half of the Strait below 300 m is only a few percentage points lower than that in the western half, the possibility should be kept in mind that turbulence in the Strait due to opposite running currents will cause some of this inflowing water to mix with the outflowing current and thus be deflected back into the Ionian Basin without fully penetrating into the Adriatic. This process would tend to reduce the horizontal gradients across the Strait.

It had been suggested previously that, because of the shallowness of the Adriatic, its water structure closely follows the fluctuations of the existing weather regime. By the same line of reasoning it appears highly probable that the circulation through the Strait of Otranto is also directly affected by changes in wind direction and intensity. Southerly and southeasterly winds tend to drive more surface water into the Adriatic. An excess inflow of this nature must be compensated for by an increased outflow which can then take place only in subsurface layers.

SUMMARY

1. Below 1600 m the water in the center of the Ionian and Levantine basins is identical in temperature and salinity structure. The amount of dissolved oxygen at these depths is consistently higher in the Ionian Sea by about 0.15 ml/L.

2. No evidence was found of a subsurface flow of Aegean water into the eastern Mediterranean via the three channels between the island of Crete and Asia Minor. Due to the high salinity and oxygen values in the southern Aegean, below the sill depths of these channels, such an effluent, if it existed, would be readily detectable in the Mediterranean stations. A similar situation was found in the channels into the Aegean, located between Crete and the Greek mainland.

3. The water entering the Ionian Sea through the Strait of Sicily was eliminated as a major component of the deep water of the eastern Mediterranean. The somewhat fresher water flowing out of this Strait is separated from the deep water by a permanent intermediate layer having a higher salinity than the layer below it. The Strait of Messina was ruled out as a factor in this problem because of its shallow sill depth, narrowness, and the tidal nature of its currents.

4. The Adriatic Sea, the only other possible source of deep eastern Mediterranean water, has a complicated water structure. Due to its restricted size and shallow mean depth it is particularly susceptible to short term weather fluctuations. Thus, single sections or stations cannot be considered representative of average conditions for any particular season. Nevertheless, three sections across the Strait of Otranto indicate an outflow of Adriatic water on the bottom and western side of this Strait. This is consistent with the dissolved oxygen distribution in the entire eastern Mediterranean. There is generally a minimum value at mid-depths, with a secondary maximum below it wherever the bottom is deep enough. In both the minimum and maximum oxygen layers the highest values are found near the Strait of Otranto and along the western edge of the Ionian Sea. This oxygen pattern suggests a counterclockwise circulation in the deep water of

the eastern Mediterranean, with Adriatic water hugging the bottom as it enters the northwestern Ionian Sea and gradually rising to mid-depths as it is replaced by newer water from the same source. An analysis of one station in the Adriatic, occupied on 12 occasions, shows that, during a majority of the time, water at depths of the sill in the Strait of Otranto has a higher potential density than the deep water of the eastern Mediterranean and can therefore flow downslope into the Ionian Sea. This water is composed of relatively fresh water, largely river effluent from the northern Adriatic, and of Ionian Sea water of relatively high salinity from intermediate depths and of variable salinity from the inflowing surface layer. These component water masses are mixed in the southern Adriatic, particularly by surface cooling and vertical convection in winter. The resultant mixture gradually sinks to the bottom and flows slowly out of the Strait of Otranto back into the Ionian Sea. There seems little doubt that this outflow is quite irregular, depending to a large extent on the prevailing weather regime.

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